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THE REGULATION OF EYE POSITIONS AND MOVEMENTS INDUCED BY THE LABYRINTH.

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CHAPTER I.

Tonic Labyrinth Reflexes on the Eye.

I. The bearing of the eyeball in the orbita is determined in all animals by reflexes. In the higher mammals these reflexes are predominantly visual, and labyrinthine stimulation is of minor importance. In mammals like the rabbit, however, where the visual reflexes, if existing, are weakly developed, labyrinthine stimulation plays the leading role.

The labyrinthine reflexes determining the position of the eye in the orbit have been referred to under various names, for example: compensatory eye movements, eye position (postural) reflexes, and tonic eye reflexes. Compensatory means that an eye movement resulting from a head movement occurs in the opposite direction, so that the identity of the field of vision remains more or less preserved in spite of the head movement. It is highly desirable that we distinguish between compensatory eye movement and compensatory eye positions. Nystagmus illustrates the former, tonic reflexes is a good synonym for the latter.

Compensatory eye position seems to have been known in antiquity. But the first measurement of the rolling following head rotation

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round the bitemporal axis was made by v. Graeffe[25] in 1854. Nagel[37] shortly afterwards made a contribution to the same problem. Hoegyes[27] carried out a study on compensatory eye positions in 1885, which, however, became easily accessible to scientific readers only in 1912. His observations included the cases of body rotations round the longitudinal axis, and they require but a few corrections. they are, however, only qualitative. Later investigators are Kubo[40], Bárány[3, 4, 5], Rothfeld[60], van der Hoeve and de Kleyn[28a], Fleisch[23].

The reason why the earlier descriptions did not sharply distinguish between motion reflexes and tonic reflexes is probably found in the fact that little was known about the origin of these reflexes. Mach and Breuer were the first to point out that all these reflexes were of labyrinthine origin, and that the labyrinth could be stimulated by both position and movement of the head. With Breuer this doctrine was deduction from his theory of the functioning of the labyrinth. In agreement with Mach, he assumed that the postural reflexes had their origin in the otolithic organs. Nagel and Hoegyes demonstrated experimentally that extirpation of both labyrinths brings about failure of the compensatory eye positions.

Graeffe made the assertion that the eyeball rolls round an axis which is perpendicular to the plane in which the bellies of the oblique muscles lie, but this seems to be incorrect. Nagel was the first to point out that the position of the eyeball is not exclusively determined by the just preceding motion of the head, so that it may be slightly different if the head has reached its position from one or the other direction. This was confirmed by observations of Delage on human beings.

Hoegyes described the compensatory eye positions in the following way:

Turning the rabbit's head dorsally round the bitemporal axis causes a rolling backwards accompanied by a vertical deviation downwards and a slight horizontal deviation forwards.

Turning the head ventrally round the bitemporal axis causes a rolling backwards accompanied by a vertical deviation upwards and a slight horizontal deviation backwards.

Turning the head round the longitudinal axis causes the eye which lies underneath to assume a vertical deviation upwards accompanied by a slight rolling forwards and a slight horizontal deviation backwards. The other eye shows an opposite change of position. Hoegyes made a distinction between the beginning and later phases of a head rotation; when the bitemporal axis is functioning, the rolling motion takes precedence over the vertical and horizontal displacements, and

when the longitudinal axis is functioning, the vertical displacements take precedence over the rolling motion and the horizontal displacement. Here I want to contradict him. All three components are effective from the beginning.

The motor effects reach their maximum when the head has rotated, round any axis, about 90 degrees. At 180 degrees the eyeball returns to its initial position in the orbit.

Hoegyes sharply distinguished between motion reflexes and tonic reflexes. He taught the necessity of waiting until the nystagmus has ceased before trying to describe the displacements. If one uses the displacements of the eyeball as data, one can then compute the bearings of the head in space (loc. cit., p. 721 and p. 1382).

Kubo was puzzled by his observation that to the supine position of the head the eyeball seemed to respond somewhat ambiguously. The explanation was given by Bárány when he discovered the preprioceptive reflexes originated in the neck. The condition of the neck muscles in the supine position of the head causes strong rolling displacements.

Rothfeld studied the displacements within 90 degrees around the bitemporal axis, from the normal position of the head to the position:—head vertical, muzzle upwards. He agreed with Nagel that only near the normal head positions can the displacement of the eyeball be said to be constant. In other head positions the displacements of the eyeball become uncertain, although the uncertainty is only of a few angular degrees only.

New measurements by a photographic method were made by van der Hoeve and de Kleyn. They concerned themselves with the three fundamental axes of rotation assumable in space. They seem to have a tendency to regard as negligible small displacements and to schematize the grosser displacements. In the curves published by them, the smaller displacements which they neglect are visible. They disagree with Nagel as above where Rothfeld agrees with him.

Fleisch determined the motion of a ray of light which was reflected from a mirror fastened to the eyeball, while the cornea was made impervious to light. His observations are the best in the literature. He confirmed Nagel's observation that the angle of placement of the eyeball depends also on the direction of the just preceding motion of the head. The same has been confirmed by me[42, 44] and by Fischer[20].

II. I have taken up again the study of the tonic reflexes previously made by me and have applied photographic registration (see Fig. 1). The reader should be familiar with the work of Nagel, van der Hoeve and de Kleyn and Fleisch.

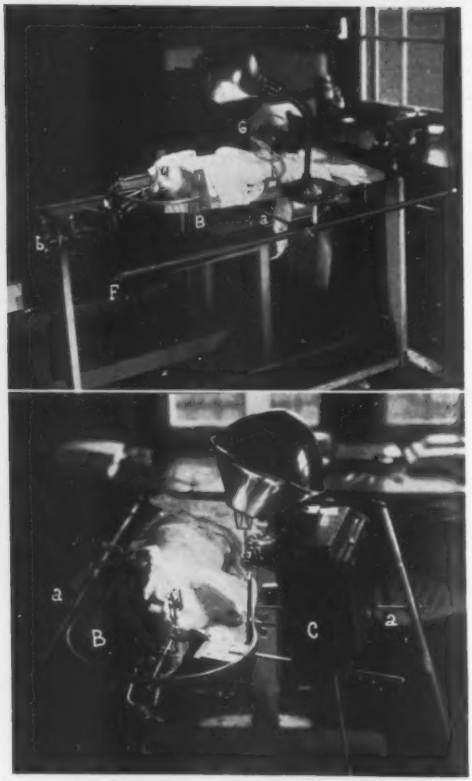

Fig. 1 shows the technique for recording photographically the tonic reflexes on the eye.

(F)—iron frame which holds the rabbit board (B); (a) and (b) the axes of the frame. (C)—photographic camera. (G)—wheel for determining the inclination of the board. In both photographs the small frame before the eye is clearly seen.

The bitemporal rotation takes place on the axis (a); the longitudinal rotation on the axis (b); the dorsoventral rotation on the axis (b), after having turned the rabbit board 90° upwards on the axis (a) (cfr. Fig. 5).

1. Eye Position While the Head Rotates Round the Bitemporal Axis (Figs. 7 and 10, I and II).

The head is raised: The eye rolls orally and is displaced ventrally and orally.* The maximum occurs when the head registers between 90° and 135°. From here to near 180° there is a slow change. Further on the eye quickly rolls caudally and reaches the maximum of the rolling backwards between 220° and 270°.

The head is turned down: The eye rolls strongly caudally and is slightly displaced dorsally and caudally. The maximum occurs in the neighborhood of 270°. For a long while there is little change until near 180° the eye returns quickly to its initial position.

Studying now the rabbit's field of vision, we find that the compensation has been imperfect. The total field of vision consists of two parts located on both sides of the head. The center ray of either of these two partial fields would have to stimulate the center of the retina all the time if we were to speak of true compensation. Such is not the case. When the head is lowered, the optical axes diverge more than before; and when the head is raised, they tend toward convergence. If we are willing to overlook this change of divergence, we can still speak of compensation.

One can regard these changes of the total field of vision as advantageous for the animal. When the head is lowered, the total angle of the world behind the animal which is now covered by the field, is a little greater. While eating, the animal can more easily notice enemies which approach from behind. When the head is raised, on the other hand, the ground directly in front is more likely to remain visible, to be stepped on with security.

It would be interesting to know if these changes of divergence are accompanied by changes in accommodation.

In accordance with what we said of Hoegyes, the compensation would be perfect in the beginning and would deviate from perfection in the useful manner just described, only when the head is raised or lowered extremely. But in this assertion Hoegyes is wrong. The compensatoriness of the adjustment is imperfect all the time, from the very beginning of the head movement.

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*Rolling of the eye means a rotation round the visual axis (in German, Raddrehung); the direction of the rolling is referred to the upper pol of the cornea. Vertical motion is a rotation round the horizontal axis of the eye. Horizontal motion is a rotation round the vertical axis. Normal position of the head is that position which is used by the rabbit while resting. In this position the external semicircular canal lies horizontally in space; the mouth about 35 below the horizontal line (see Fig. 7, I, 1). Normal or primary position of the eye is the position assumed by the eye when the head finds itself in the normal position (see Fig. 7, II, 1); any other position of the eye may be called secondary position.

Naturally one finds slight individual differences among the rabbits, but no essential differences in the manner of adjustment. The deviations from the usual adjustment, which Nagel observed as dependent on the just preceding motion, amount only to a few angular degrees.

About rolling motion, all authors are in this agreement. In the neighborhood of the normal position of the head the degrees of the rolling and of the head rotation are about the same; in the sector 270°-0°-90° the direction is the reversed and in the sector 90°-180°-270° the direction is the same. Further is to be said that the eyeball changes cannot be expressed by a simple mathematical equation, such as of an ellipse, parabola, hyperbola, sine or cosine. Small parts of any record curve can always be thus expressed. But that is of no significance.

2. Eye Position While the Head Rotates Round the Longitudinal Axis (Figs. 11 and 13, I and II).

The displacements of the eyeball are, as stated in the historical part, related to each other as required by the fact that when one eye goes down, the other goes up. The vertical compensation prevails, but the other two components are not negligible and doubtless of advantage for the composition of the total field of vision. The lower eye sees more of what goes on behind and the upper eye more of what goes on in front.

CHAPTER II.

Tonic Labyrinth Reflexes on the Eye Muscles.

I. Current Ideas on the Physiology of the Eye Muscles.*

In the physiology of the eye muscles there are still many unsolved problems, and we may again quote Hoegyes' words in the introduction to the exposition of his findings[27, p. 1361].

"There are several methods for determining which muscles take part in the production of the eye movements. This is not the place to discuss the advantages and disadvantages of each method. The fact is that until now neither with the help of one nor the other method has it been possible to ascertain which muscles participate in the different eye movements; theoretically it is possible to calculate for each muscle all possible combinations of eye motions, but we have no definite criterion as to which of these motions actually takes place."

The following four methods have been used to ascertain the function of the eye muscles:

1. The function of the eye muscles is deducted from their anatomical structure, and on the basis of the estimated action of each of the six muscles it is calculated which muscles take part in the production of the different eye movements.

Generally it is accepted that the fascia (the capsul of Tenon and the fascia of the muscles) hold the eye in such a way that any translation movement is made impossible; the center of the eye does not change its position in the orbit and, therefore, the eyeball may accomplish only rotations. However, sometimes the idea has been expressed that the muscles play a role in the fixation of the rotation center of the eye; F. B. Hoffmann[29, p. 259] states: "The bulbus is not a freely movable body, the ligaments and the muscles hold it in place in the fat-padded orbit; the straight muscles pull the eyeball backwards against the fat cushion; a component of the force of the oblique muscles pulls the bulbus forwards. Also the ligaments help."

This question has not been further studied, as far as I can see, until Maxwell and Huddleston and I found experimental facts which

*It is not intended to give here a complete exposition of the problem, but only of those fundamental ideas, which may help to understand the facts described in the following chapters. The reader may consult for further information the papers of Zoth[65], F. B. Hoffmann[29], Cords[17a] and Tschermak[56].

cannot be explained by assuming that the center of the eye is being fixed by noncontractile tissues.

In order to simplify the problem and be able to calculate the action of each muscle, it is accepted that the muscles can be considered as thin threads, geometrical lines, extended between the centers of both insertions. The perpendicular through the center of the eye to the plane determined by the straight line representing the muscles and the center of the eye is called the axis of the muscle. The action of each muscle consists in rotating the eye round this axis. Numerous schemes demonstrating graphically the activity of the eye muscles have been published; the best ones seem to be those of Ruete[65] and Márquez[28]. These schemes show that the axis of none of the muscles exactly corresponds to one of the fundamental axes of the eyes, and, consequently, each muscle must have, in addition to its main action, some other action; for instance, a muscle may produce, in addition to a vertical movement of the eye as its main action, a slight rotary movement as its secondary action.

If several muscles combine their activities the problem becomes much more complicated because the movement of the eye brings forth a passive stretching of several muscles and, consequently, the eye finds a resistance of determined direction against the movement; to calculate these resistances is a very difficult task, as there are no reasons to assume how behave those muscles, which are not actively participating in the production of the eye movement. Even is it very difficult to calculate the action of the contracted muscles; when the eye moves, the muscles change their direction, and, therefore, may have quite other actions than in the primary position of the eye. Recently van der Hoeve[28] has calculated the action of each muscle in different eye positions and obtained very complicated results; he accepts as basis for his calculations that the eye muscles can be represented by straight lines.

In this case, however, it seems that to consider the eye muscles as straight lines instead of simplifying the problem gives rise to a complication. Helmholtz[68] brought to attention the fact that the insertions of the eye muscles are wide and, consequently, the force of the muscle may act in each position of the eye on a different point of the insertion; according to this, the activity of the single muscles during the eye movement may undergo only a slight change.

On the other hand, we must bear in mind that, as Hering and Hoffmann[29] have pointed out, if several muscles contract at the same time, their secondary actions may be reciprocally compensated and their principal action remain constant.

Hoegyes was the first who tried to ascertain which eye muscle brings about the labyrinthine reflexes. He determined first the action of the individual muscles and calculated then which muscles produced the tonic labyrinth reflexes. He assumed that if the eye moves in a certain direction only those muscles contract whose action corresponds most closely to the eye movement. He put the results of his calculations into several tables, which at present have only a historical interest, as in them only the contractions of the muscles and not their relaxations were taken into consideration.

Later have tried among others, Rothfeld[60], Bárány[5], Ohm[58], Mendoza[56] and Ivy[34] on the ground of the mentioned theoretical methods, to determine the correlations between the ampulla of the semicircular canals and the eye muscles. In the calculations of these authors may be found some very important data, at the same time, however, also incorrect assumptions. These tables were arranged on the ground of accepting that the eye nystagmus is brought forth by one or two muscles. Also it was accepted that each semicircular canal is connected only with one or two muscles (according to the law of reciprocal innervation, two or four). The experimental study of the problem failed to give a support to these calculations[48, 49].

2. The second method for the examination of the eye muscle mechanism consists in building an artificial eye model.

In the literature this method was used by Magnus and de Kleyn[53]. But their curves do not correspond with the activity of the muscles in the living eye, because it is impossible to reproduce in a model all the details of the living tissues[41].

3. The third method consists in studying the modifications in the eye movements when one or several muscles are made inactive. To this method belong the study of clinical cases and experiments with section or extirpation of one or several muscles.

A systematic investigation on the function of the oblique muscles in rabbits was accomplished by v. Graefe; he severed one or both oblique muscles and left the recti intact, or severed the recti without damaging the oblique muscles. These experiments were repeated with the same results by Hoegyes. After the oblique muscles are cut, the rolling of the eyes disappears, but it still is present after the four recti are cut. Each of the oblique muscles is sufficient to let the eye roll in both directions, however, the rolling in the direction of the severed obliquus is smaller than before the operation. The rolling is then being brought about by alternative contractions and relaxations of the remaining obliquus. Magnus and de Kleyn[52, p. 170] confirmed the observations of v. Graefe and Hoegyes. Kubo also studied

in rabbits the tonic labryrinthine reflexes after cutting through one or several muscles.

The most important experiments, however, seem to be those of Sherrington[61], which brought him to extend the law of reciprocal innervation to the ocular muscles.

He found with monkeys after cutting the third and fourth nerves the external rectus relaxed when an abduction movement of the other eye took place, *i. e.*, that the external rectus relaxed when the internal rectus contracted.

These experiments were, however, not sufficient for deducting the laws regulating the co-ordination of the eye muscles; for instance, v. Graefe could not account for the participation of the straight muscles in the rolling, and in the same way the experiments of Sherrington could not account for the participation of the vertical and oblique muscles in the horizontal movements.

4. The fourth method of examination of the function of the eye muscles consists in studying the contractions and relaxations directly on the eye muscles. The bulbus is extirpated, and the reactions of the muscles to the excitation (of the nervous system, labyrinth or neck nerves) which brings forth known eye movements, are recorded.

This method was for the first time used by Topolansky[64]; he studied in rabbits the reactions of the horizontal muscles to faradic stimulation of different parts of the cortex and thalamus. The tracings in the paper of Topolansky were very poor. Bartels[10, 11] described a perfect technique and studied in rabbits the reactions of the horizontal muscles to vestibular excitations (rotation, caloric nystagmus and galvanic stimulation).

Bárány together with Vogt (C. and O.)[8] studied in monkeys the reactions of eye muscles to the stimulation of the cortex; P. Hoffmann and O. Koellner[31] have studied in rabbits the activity of the eye muscles following galvanic excitation of the acoustic nerve. De Kleyn[36, 37] repeated some of the experiments of Bartels and studied the neck reflexes on the horizontal muscles.

In 1925-28 I conducted systematic experiments on the reactions of all the eye muscles to different kinds of stimulations[41-50] (rotation innervation, caloric nystagmus, extirpation of one labyrinth, plugging or isolated stimulation of one semicircular canal, excitation of the conjunctiva, lesions in the medulla and brain stem, faradic stimulation of the corpora quadrigemina, etc.) and in recent years there appears a number of publications[12, 13, 66], in which the curves of reactions of the eye muscles, mostly of the horizontal ones, are described. A special mention deserves the paper of Maxwell and Hud-

dleston[55], who have studied in dogfishes the reactions of all the eye muscles to stimulations of the ampulla of the horizontal canal. They found "that each excitation of a horizontal ampulla calls forth, in addition to the response of the appropriate external or internal rectus muscle, a smaller but very definite contraction of each of the four other muscles" (p. 445). The reactions of the horizontal muscles obey the law of reciprocal innervation. For the simultaneous contractions of the four other muscles Maxwell and Huddleston account in the following way: "The movements of the eyeball in response to stimulations of the horizontal ampulla gives, indeed, the appearance of rotation of the bulb round a fixed vertical axis in which case none other than the two rectus muscles would need to participate" . . . "It is obvious, however, that no such vertical axis . . . has any anatomical existence, a fact which has recently been very clearly and forcibly stated by Lorente de Nò[41]. Either the eyeball must be pulled about on its fatty cushion in the orbit in an unsure way or else some or all of the other ocular muscles must by appropriate tonic contraction serve as fixation muscles[11] (p. 443). During the horizontal eye movement, as mentioned above, the other four muscles contract and "since the superior oblique and the superior rectus are attached nearly to the same point of the upper side of the bulb, and the inferior oblique and inferior rectus are similarly attached to the lower side of the bulb, the simultaneous contractions of all four must have a fixation effect with the result that the mechanism acts as if a real vertical axis had been provided" . . . (p. 446).

The law of reciprocal innervation of antagonistic muscles has been often discussed; however, no definite conclusions were reached. Firstly, it is very difficult to give a good definition of antagonistic muscles embracing all cases of muscle activity; on the other hand not sufficient experiments have been carried out; the few data available before the publication of my papers were obtained with experiments on horizontal muscles in the case of cerebral or labyrinth excitations bringing forth horizontal movements; in such cases the law of reciprocal innervation is almost always valid (see Chapter VII), as Schnabel, Sherrington, Topolansky, Hoffmann[30], Bartels, de Kleyn, Huddleston and Foe[33], Undritz and myself pointed out. The experiments of Sherrington, although subjected to criticism by Tillney and Pike[63], seem to have given correct results.

There are, however, other cases where the law of reciprocal innervation does not hold true (see Chapters III, IV and VII), namely, when the muscle contractions do not produce an actual eye movement; in my first publication on this subject I perhaps did not state

clearly enough the cases in which this law is valid and those in which it is not, but as early as 1926 I made quite definite statements[45], and explained when and why the so-called antagonistic muscles are innervated as synergists. We shall take up again this problem in Chapters III and VII.

DIRECT EXPERIMENTS ON THE EYE MUSCLES.

II. Preliminary Anatomical Remarks.

The anatomy of the eye muscles has been described very satisfactorily by Wessely[67], Magnus and de Kleyn[55]. Wessely gives a good illustration.

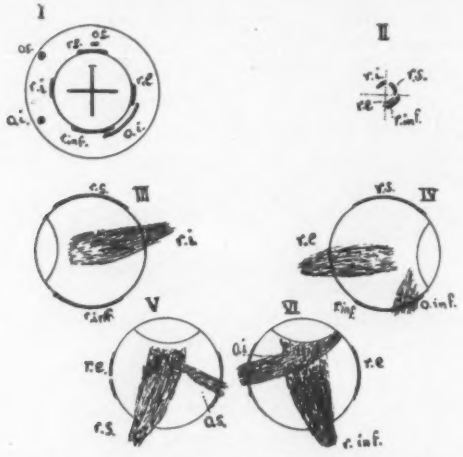


Fig. 2. Anatomy of the eye muscles in the rabbit. Left eye.
I.—Position of the insertions of the muscles on the eye.
II.—Position of the insertions of the muscles on the bone.
III-IV.—The different eye muscles (in III and IV—the muscles of the right eye have been represented), r. e.—rectus externus; r. i., rectus internus; r. sup.—rectus superior; r. inf.—rectus inferior; o. s.—obliquus superior; o. inf.—obliquus inferior. In III-IV the vertical muscles and in V-VI the horizontal muscles have been represented as a thick line showing the part of the muscle which lies on the eyeball.
III and IV are side views of the eye; in V the eye is in a view from above, and in VI in a view from below.

In addition to the retractor the rabbit has the four rectus and the two obliquus muscles. The rectus muscles have their origin on the bone around the foramen opticum, as shown in Fig. 2[44]. On the other hand, the vertical muscles are inserted close to the rim of the cornea. Their tendons are very short. The horizontal muscles have slightly longer tendons and are inserted a trifle more backwards.

The oblique muscles run from the trochlea forward, unlike the corresponding human muscles, and are inserted near the rim of the cornea, the upper one under the rectus superior and the lower one between the rectus inferior and the rectus externus. The muscles do not form, as in human anatomy, a funnel filled with adipose tissue, but lie close to the eyeball, separated from it only by the retractor.

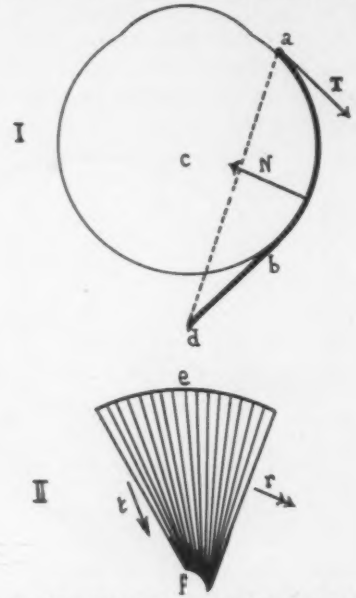


Fig. 3. Scheme to show the forces developed by the contraction of the straight muscles (I). The muscle (a, b, c) when it shortens tends to become a straight line (a, d) and to approach the insertion (a) on the eye to the insertion (d) on the bone. If the center (c) of the eye is fixed, the eye will rotate in the direction of the arrow (T) (tangential force of the muscle). If the center of the eye is not fixed, as it really happens in the living eye, the combined action of the forces (T and N) (N, normal force of the muscle) will produce in addition to a rotation a translation of the eyeball.

II. Diagram representing one of the straight eye muscles of the rabbit. (e) is the broad insertion on the eye; (f) the narrow insertion on the bone; both insertions are not parallel and therefore if the muscle contracts it will tend to move the insertion (e) towards the insertion (f) in the direction of the single headed arrow (t) (tangential force) and to rotate the insertion (e) in the direction of the double headed arrow (r) (rotary force of the muscle) until both insertions become parallel.

As in the rabbit's eye the muscles are always in a certain state of contraction; the combination of the forces (t, n, and r) developed by the six muscles holds the center of the eye in a fixed position (cfr. Fig. 24).

The eye muscles of the rabbit are broad ribbons drawn over the eyeball. Their pull must not be conceived as acting along a straight line drawn from one end to the other. Several effects have to be considered as likely (see Fig. 3):

a. The contracting muscle acts tangentially on the eyeball (see Fig. 3, I.

b. The contracting muscle pushes the eyeball strongly in a normal direction, as shown by Fig. 3, I.

c. Each rectus muscle forms a ribbon which is very narrow at the bone insertion and rather broad at the eye insertion, as shown in exaggerated form in Fig 3, II. The contraction of the rectus therefore not only rotates the eyeball backwards as indicated by the simple arrow of the figure, but also rolls the eyeball round the optical axis, although only slightly, in the direction indicated by the double-headed arrow of the figure.

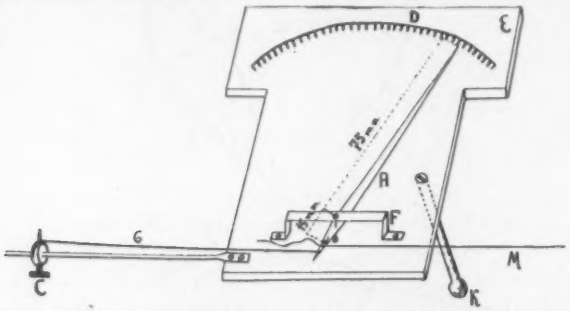


Fig. 4. Scheme of the apparatus used for measuring the isotonic contractions of the eye muscles during slow rotations of the head on a horizontal axis. (M) thread to the muscle; (G) rubber thread, the length and tension of which may be regulated by means of the screw (c). (F) frame holding the axis of the aluminum lever (A). (D) scale.

III. Technique.

1. The first direct study on tonic changes occurring in the eye muscles in consequence of changes in head position was carried out by me[41]. The eyeball was removed. Threads were tied to the muscle ends and the contractions in various positions were observed.

2. I also used the method, which Hoegyes and Kubo had used previously, of cutting one or more muscles and observing the resulting changes in the eye reflexes.

3. In order to measure the shortening of a muscle, I made it act on a very light and balanced aluminum lever which pointed along a circular scale[42, 43, 44] (see Figs. 4 and 5). The muscles were kept gently stretched by rubber threads, the pull of which is determinable and remains virtually constant. The whole recording instrument was attached to the Czermak clamp holding the head. The body of the rabbit is tied to the board on which the Czermak clamp is fastened. The whole board with animal and instrument on it can then be rotated as desired.

It is important that the muscles are stretched by the rubber thread in their natural directions from their origins. Even a strong jerk of the board does not change the zero point of the aluminum lever if all necessary precautions have been taken.

It is not difficult to build the registering instrument with six levers and six scales, so that all muscles can be recorded at once. But I found it usually more convenient to record only two or three muscles at a time.

The rotation axis has always been horizontal, but as I have used two different postures of the animal as starting positions for the rotation: head in the normal position and head in the vertical position with the muzzle pointing upwards—the rotation of the rabbit

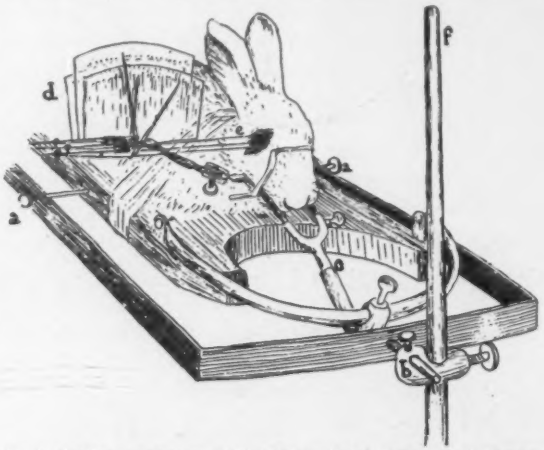


Fig. 5. A similar apparatus (d) having three levers and three scales as used by my coworker, E. Hartmann (Acta Otolaringol., 1927) and by me (Monatsschr. f. Ohrenheilk., 1927).

has been alternatively on the bitemporal, oral-caudal (longitudinal) and dorsal-ventral axes (see Figs. 1 and 5).

The board on which the animal rested was turned quite slowly, some time was given for any motion reflex to fade out, and then the change of the length of the eye muscle measured. After twenty-four or twelve readings, corresponding to sector magnitudes of 15° or 30°, the standard position of the animal was regained.

4. An automatic method of registration is the following[45, 49]: The same board which carries the animal also carries a kymograph. In this case a graph is obtained directly (see Fig. 6). The longitudinal axis of the body of the rabbit was always parallel to the rotation

axis, but the head was held in two different positions, in the normal position (longitudinal rotation) or bent upwards 90° round the bitemporal axis (dorso-ventral rotation).

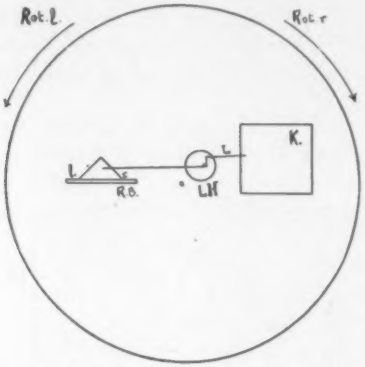


Fig. 6. Diagram showing the arrangement of the rabbit board and the kymograph on a turn table rotating on a horizontal axis. (T) turn table; (R. B.) rabbit board; (r. l.) right and left side of the rabbit; (K.) kymograph; (LH) lever holder; (L) writing lever. The arrows show the direction of the rotation, Rot. r. towards the right, Rot. l. towards the left.

IV. Data Obtained After Cutting One or Several Muscles.*

In order to avoid repetition I reproduce here only four experiments:

A. Eye Positions During the Slow Rotation of the Head Round the Bitemporal Axis.

a. The Reflexes After Cutting the O. Inf. and Then the O. Sup. (Fig. 7).

*A preliminary remark about these experiments is necessary. The cutting of one muscle changes the whole force system of the eye muscles, on the one hand, because some forces are withdrawn and, on the other hand, because the muscle which has been cut does not withstand the pressure of the retro-ocular tissues. In rabbits this pressure is very changeable as the blood filling varies greatly with the changes of the position of the animal in space. It is, however, almost constant when the animal is in a horizontal position or in a vertical position with the muzzle pointing upwards. But the blood filling increases considerably when the rabbit is held vertically with the head pointing downwards. This will not influence our experiments as we shall consider mainly the eye reflexes in those positions in which the blood filling remains almost constant. If the blood filling is increased caution is needed because even a muscle in a state of maximal relaxation offers a considerable resistance against the pressure of the retro-ocular tissue. When one straight muscle is cut through close to its insertion on the eye it may still exercise a certain force because its fibres remain connected with the capsul; therefore we must interpret the modification of the eye displacements after cutting one muscle as the result of diminution of the force developed by it. This explains why, after cutting the vertical muscles, the eye does not show in the normal position of the head pronounced spontaneous vertical displacements; as easily seen, the fact that the severed muscle may still exercise a certain force on the eye strengthens the conclusions drawn from the experiments.

With the obliquus muscles the case is somewhat different as the cutting of the muscle is made not close to the insertion but through the belly of the muscle and therefore the severed muscle remains totally out of function.

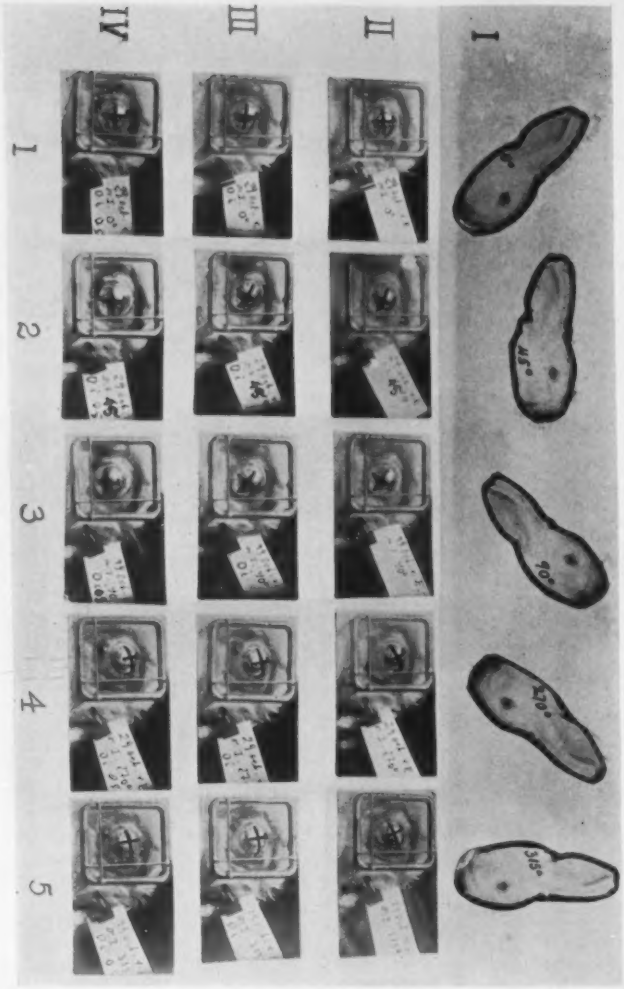


Fig. 7. Tonic labyrinth reflexes on the eyes in the normal eye (II) and after having cut the inf. obliquus (III) and both obliquus muscles (IV). I, shows the positions of the head, II, III, IV the positions of the eye; the photographs of the eye have all been placed in the same way; therefore, the deviations of the eye are always referred to the starting position of the head (I,1).

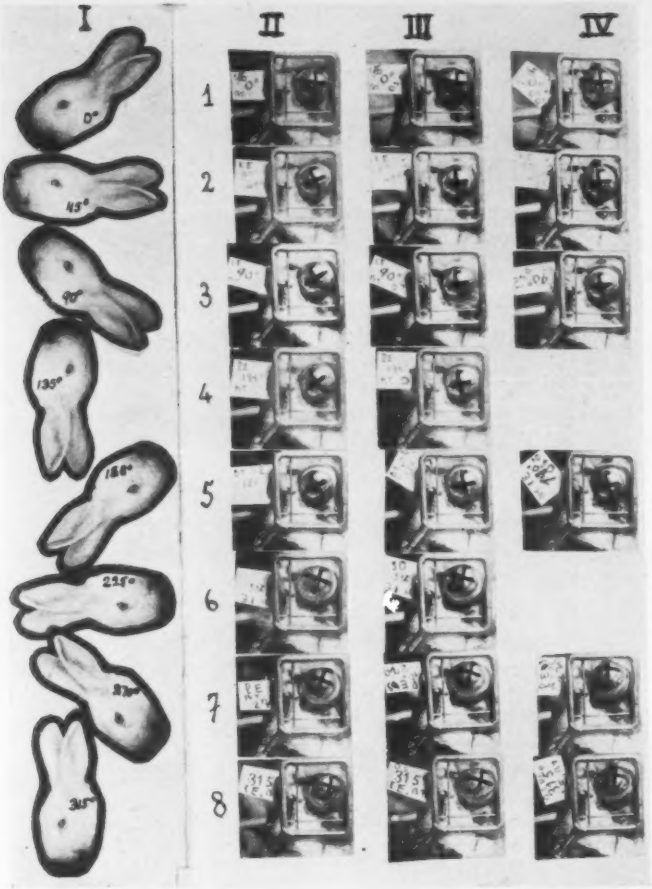


Fig. 8. The same after having cut the obliquus superior or both oblique muscles. I shows the positions of the head, II the positions of the normal eye, III after having cut the superior obliquus, and IV after having cut both obliquus muscles.

After the o. inf. (see Fig. 7, III, 1) has been cut through the eye rolls spontaneously somewhat forwards; we may conclude from this that the o. inf. was in state of slight contraction and exercised a certain force against the other muscles.

If the head is lowered (see Fig. 7, III, 5, 4) the eye rolls only a few degrees backwards. This rolling consists mainly in the dis-

appearance of the spontaneous rolling forwards. A relaxation of the o. sup. during the rolling backwards is therefore highly probable; on the other hand, the activity of the o. inf. is absolutely necessary in order that the rolling backwards may take place. The eye shows in III, 4, 5, a strong lifting and a slight horizontal deviation backwards. The strong lifting points to a contraction of the r. sup. A considerable protrusion of the bulbus is also to be found, therefore we may conclude that the o. inf. was offering then a resistance against the pressure of the retro-ocular tissues.

If the head is lifted (III, 1, 2, 3) the eye rolls forwards, apparently in the same way as before the operation; however, if the eye positions are being carefully studied important differences may be observed. The rolling is stronger by a few angle degrees than before, but the vertical deviation downwards and the horizontal deviation forwards are somewhat less. We may conclude from this that the o. inf. exercises a considerable force in this position of the head, because otherwise its cutting would not have influenced the position of the eyes.

After the o. sup. (IV, 1-5) has been cut the spontaneous rolling forwards disappears (IV, 1) and the vertical axis of the eye assumes again its vertical position in space. We may conclude from this that the o. sup. in the primary position of the eye was in a certain state of contraction and, on the other hand, that the activity of the straight muscles tends to retain the eye in the primary position.

If the head is lifted (1-3) or lowered (5-4) the eye shows a minimal rolling in the same direction as before the operation; this points to the fact that the *rectii have a certain rolling activity* and that contractions of these muscles combine in such a way that they assist the action of the oblique muscles.

That the vertical muscles play an important role is shown further by the considerable vertical and horizontal deviations of the eye (IV, 1-5) we may conclude with great probability that the r. inf. contracts during the rolling of the eye forwards and the r. sup. during the rolling of the eye backwards.

b. The Reflexes After Cutting the O. Sup. and Then the O. Inf. (Fig. 8).

After the o. sup. has been cut the eye rolls spontaneously somewhat backwards (III, 1); from this we may conclude that the o. sup. was before the operation in a state of slight contraction. If now also the o. inf. is cut the vertical axis of the eye assumes again its vertical position (IV, 1).

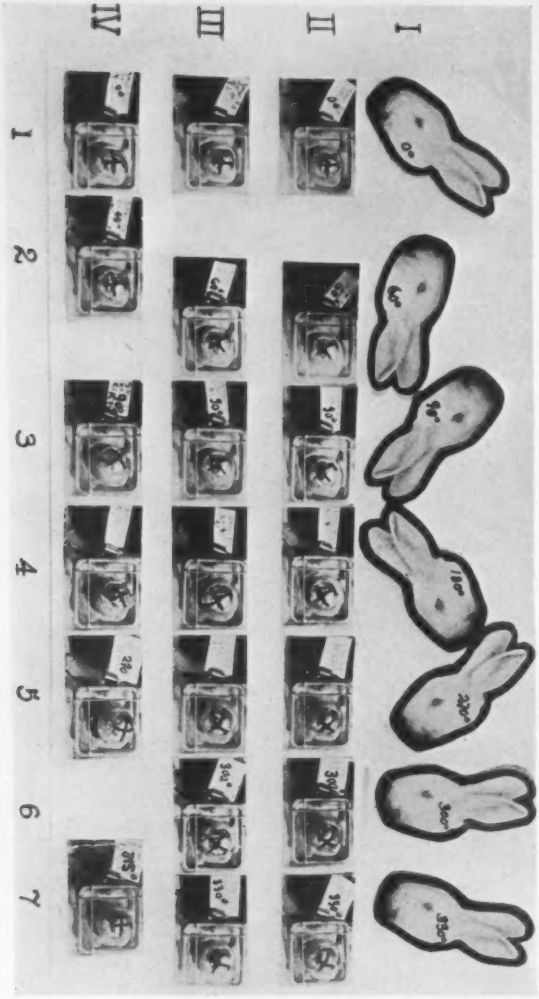


Fig. 9. The same after having cut the sup. rectus (III) and both vertical muscles and the inferior obliquus (IV). I—head positions; II—eye positions before the operation; III—the same after having cut the superior rectus; IV—the same after having cut the inferior rectus and the inferior obliquus.

After the o. sup. has been cut the eye can still accomplish a small rolling forwards (III, 1-5) but this rolling slightly increases after

the o. inf. is also cut (IV, 1-5). We may conclude therefrom that the rolling forwards is produced mainly through contraction of the o. sup.; however, we have no right to assume that the o. inf. relaxes; on the contrary, there are good reasons to believe that the o. inf. exercises a considerable force during the rolling of the eye forwards. The straight muscles assist the o. sup. in bringing forth the rolling.

If the head, after the o. sup. has been cut through, is being lowered (III, 8, 7, 6) the eye rolls backwards, almost as much as before the operation; this brings us to the conclusion that the o. sup. relaxes. After the o. inf. has also been cut (IV, 8, 7 6,) there still remains a certain rolling which may be explained by the action of the vertical muscles.

c. The Reflexes After Cutting the R. Sup. and Then the R. Inf. and the O. Inf. (Fig. 9).

The cutting of the r. sup. did not produce a noteworthy change in the rolling (III, 1-7).

After the r. sup., r. inf. and o. inf. had been cut the rolling changed considerably. The eye deviated spontaneously somewhat upwards and rolled forwards (IV, 1). During the lifting of the head (IV, 2, 3) *the eye rolled only a little forwards*, although the o. sup. was active. The movement produced by the o. sup. consisted in shifting the upper eye pole towards the upper front eye angle. There certainly also took place a rolling but the movement of the eye was mainly in the vertical direction. It is important to mention that the lower eye pole protruded from the orbit. These phenomena have been observed after cutting the r. inf. (see Fig. 10, III, 2, 3); however, they are more pronounced after the o. inf. has also been cut. A very important conclusion may be drawn from this, namely that the *o. sup. only then rolls the eye sufficiently, when the r. inf. and the o. inf. co-operate in this action.* If one of these muscles or both are lacking, the rotation of the eye forwards is very defective.

d. The Reflexes After Successive Cutting of the R. Inf., R. Sup. and O. Inf. (Fig. 10).

After the r. inf. has been cut the eye shows in the normal position of the head (III, 1), a slight rolling backwards and a slight horizontal deviation, but no vertical deviation.

If the head is lifted (III, 1-3) the eye rolls forwards; the rolling is, however, not normal, as, on one hand, it is smaller, and on the other hand, it is being accompanied by a vertical deviation upwards and a slight protrusion of the lower eye pole. We have just now

Fig. 10. The same after having cut successively the inferior rectus (III), the superior rectus (IV), the inferior obliquus (V), and the superior obliquus (VII). (I) shows the head positions, (II) the reflexes in the normal eye. Figs. 7-10 represent bitemporal rotations.

stated that the action of the r. inf. is essential in order that the o. sup. may roll the eye in a normal way.

The rolling backwards (III, 6, 5) is also not quite normal, as it is accompanied by a strong protrusion of the bulbus; the action of the r. inf. in this case apparently consists in holding the rotation center of the eye by resisting the pressure of the retro-ocular tissues.

For this purpose no contraction is necessary, but only the muscle elasticity.

The cutting of the r. sup. (IV, 1) brings the vertical axis of the eye again in a vertical position in space. The rolling forwards (IV, 1-3) seems not to have changed. The rolling backwards, however, is changed; where (IV, 6) the blood filling is almost normal the lifting is not present. We may conclude from this that the r. sup. is, in this position of the head in space, in a state of contraction; in IV, 5, a lifting appears, but this does not prove anything because it could have been caused by the pressure of the retro-ocular tissues, defectively compensated by the remaining muscles.

If the o. sup. is also cut through (V, 1-6) a slight spontaneous rolling backwards may be noticed (V, 1); the eye does not roll forwards when the head is being lifted (V, 1-3). The rolling backwards (V, 6, 5) is not influenced by the cutting of the o. sup. as this muscle relaxes when the eye rolls backwards.

The photographs (VI, 1, 3, 6) show the participation of the horizontal muscles in the rolling of the eye.

In VI, 1, the eye is deviated horizontally backwards, therefore, in this position of the head the force developed by the r. ext. is greater than that of the r. int. In VI, 3, the tonus of the r. int. overweighs, as the eye deviates forwards. Because the blood filling of the orbit is here the same or even somewhat less than in VI, 1, we must conclude that the r. int. has contracted. In Fig. VI, 6, the eye is being deviated backwards; but as the blood filling here is somewhat stronger than in VI, 1, a relaxation of the r. int. would be sufficient to bring forth the horizontal deviation of the eye.

The horizontal muscles alone may cause a slight eye rolling.

Summarizing the results of these experiments we have the following conclusions:

1. When the head, by turning round the bitemporal axis is lifted, the eyes show a rolling forwards, accompanied by a vertical deviation downwards and a horizontal deviation forwards. The muscles o. sup., r. inf. and r. int. contract.

2. It is probable that the r. sup. relaxes.

3. It is probable that the r. ext. relaxes.

4. There is no reason to believe that the o. inf. shows a noteworthy relaxation; on the contrary, there are reasons to accept that the o. inf. exercises a considerable force.

5. The o. sup. needs the co-operation of the r. inf. and o. inf. in order to bring forth a normal eye rolling; when these muscles are cut the contraction of the o. sup. instead of a rolling produces a

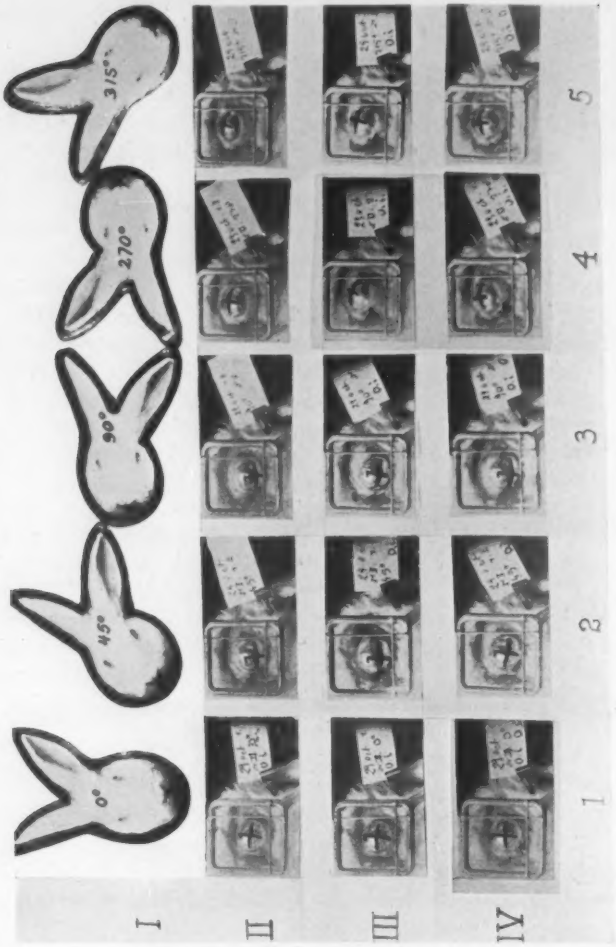


Fig. 11. Tonic labyrinth reflexes on the normal right eye (II) and after having cut successively the inferior obliquus (III) and the superior obliquus (IV); (I) shows the head position, (II) the reflexes in the normal eye. Longitudinal rotation. The same rabbit as in Fig. 7.

shifting of the upper pole of the cornea towards the upper front eye angle.

6. If the head, by turning round the bitemporal axis, is lowered, the eye shows a displacement which consists of a rolling backwards,

a slight vertical deviation upwards and a horizontal deviation backwards. The muscles o. inf. and r. sup. contract, and the o. sup. and r. inf. relax.

7. It is very probable that the r. int. relaxes; about the r. ext. we may only say that it exhibits a stronger force than the r. int.

8. Thus all muscles participate in the production of the eye positions.

9. The strong contractions of the vertical muscles must have another purpose than only move the eye in a vertical direction because the vertical excursions of the eye are only slight; this purpose must consist in preparing the rotation of the eye, in which the horizontal muscles also co-operate. The combined action of the four straight muscles holds the rotation center fixed in the orbit in such a way that the oblique muscles may only produce a rolling.

B. Eye Positions During the Rotation of the Head Around the Long Axis.

a. Participation of the Oblique Muscles.

The participation of the oblique muscles may be clearly seen in Fig. 11, III and IV.

If the o. inf. has been cut (see Fig. 11, III) the vertical deviation downwards will be less and, in addition to this, it will be accompanied by a slight rolling forwards (III, 3). This proves that the o. inf. contracts during the lowering of the eyes; it does not mean, however, that the o. sup. also contracts, because firstly the r. inf. exercises a force which rolls the eye medially and, on the other hand, the o. sup. becomes passively lengthened during the lowering.

The lifting is, in Fig. 11, III, 5, 4, somewhat greater and is accompanied by a larger rolling forwards, which may be very well explained by assuming that the o. inf. always develops a certain force, *i. e.*, that its relaxation is less than the contraction of the lifting muscles.

If the o. sup. is cut (see Fig. 11, IV), the lowering will be more pronounced (IV, 3). This proves that the o. sup. during the lowering becomes passively lengthened. The lifting takes place almost without rolling, which proves that the rolling forces of the r. sup. and r. inf. are in balance.

The participation of the oblique muscles is yet more evident in Fig. 13, IV, where the vertical muscles have been cut through, and where, consequently, the vertical movements may only be attributed to the action of the oblique muscles.

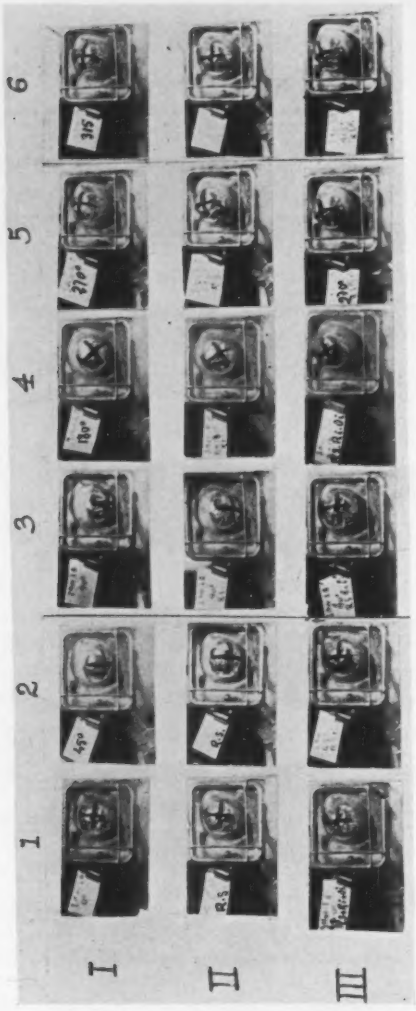


Fig. 12. The same in the normal left eye (I) and after having cut successively the superior rectus (II) and the inferior rectus plus the inferior obliquus. Head positions as in Fig. 13. The same rabbit as in Fig. 9.

The o. inf. contracts during the lowering and the o. sup. during the lifting of the eyes; however, the eye shows in Fig. 13, IV, 2, 3, and 6, 5, no worth while rolling. This may be only explained by the following circumstances: on one hand, partly by the fact that the contractions of the horizontal muscles have fixed the eyes in such a way that a rolling is made difficult, and, on the other hand, that the rolling forces of the oblique muscles are in balance. The o. sup. may relax during the contraction of the o. inf., and conversely, and their rolling forces be still in balance because the vertical movement of the eye brings forth a passive lengthening of the relaxed oblique muscle.

In any case it is very important to point out that considerable contractions of the oblique muscles do not necessarily bring forth rolling of the eye.

b. Participation of the Vertical Muscles.

The role of the vertical muscles is clearly seen in Fig. 12, II and III, and in Fig. 13, III and IV. The r. sup. contracts during the lifting and the r. inf. contracts during the lowering of the eye.

c. Participation of the Horizontal Muscles.

That the r. ext. contracts during the lowering of the eyes may be clearly seen in Fig. 13, VI, 3; but the r. int. does not show any noteworthy contraction when the eye is being lifted, because in Fig. 13, VI, 1 and 5, the horizontal deviation is almost the same. The abnormal blood filling in VI, 5, brings about a slight protrusion of the eyeball, accompanied by a slight lifting of the cornea. We may again conclude from this, that the pressure of the orbital tissues must be compensated through the muscles.

Summarizing the results we have the following conclusions:

10. If the head is inclined towards the left lateral position, the right eye shows a vertical deviation downwards, accompanied by a slight rolling backwards and a horizontal deviation forwards. In this case the r. inf., o. inf. and r. ext. muscles contract. The opposite is true for the left eye.

11. If the head is inclined towards the right lateral position the right eye shows a vertical deviation upwards, accompanied by a slight rolling forwards and a slight horizontal deviation backwards. In this case the r. sup. and o. sup. contract. It is doubtful if the r. int. shows a noticeable contraction.

12. In spite of a strong contraction of the oblique muscles the eyes show only slight rollings, because, on one hand, the vertical and horizontal recti hold the eye in such a way that the rolling is

made difficult and, on the other hand, because the rolling forces of the oblique muscles are in balance.

13. If the head is inclined towards the left lateral position the right eye deviates horizontally forwards, in spite of a strong con-

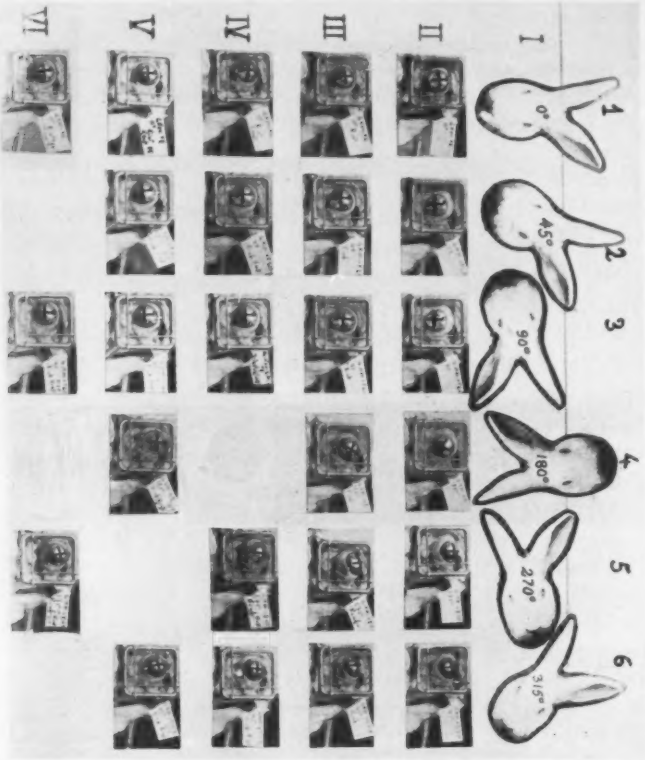


Fig. 13. The same in the normal rabbit (II) and after having cut successively the inferior rectus (III), the superior rectus (III), the inferior obliquus (IV) and the superior obliquus (VI); (I) shows the head positions; longitudinal rotation; the same rabbit as in Fig. 10. Right eye.

traction of the r. ext., because the combined force of the other muscles is stronger.

14. In every eye position, the muscle whose action corresponds most exactly to the eye deviation shows the strongest contraction. The other five muscles participate also, some with contractions, the other with relaxations. Whether or not there exists a simple law

which regulates the reciprocal dependence of the contractions and relaxations may not yet be said. The role of the muscles whose contractions don't really bring about the eye deviation consists mainly in holding the rotation center of the eye in the orbita.

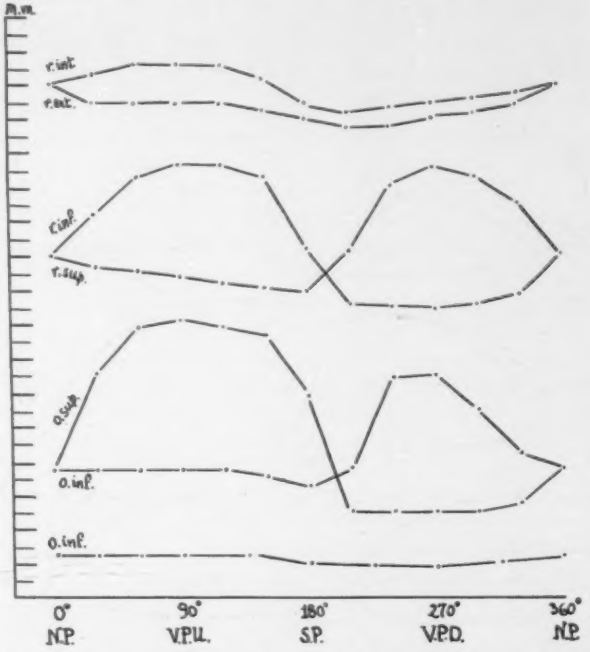


Fig. 14. Curves of the tonic reflexes of the six muscles of the right eye during the bitemporal rotation of the head. In abscissas—the head positions in angle degrees corresponding to Figs. 7-10; in ordinates — the changes in length (isotonic contractions) of the eye muscles, in m.m. The curves have been obtained with the apparatus of Figs. 4-5, recording each time the curves of two antagonistic muscles.
(N. P.) normal position; (V. P. U.) head vertical pointing upwards; (S. P.) supine position of the head; (V. P. D.) head vertical pointing downwards. These curves are also valid for the left eye. The lowest curve shows the changes in length of the inferior obliquus after having cut through its nerve (control curve). The unusual blood filling of the orbit produces in the head positions, 180°-270°, a small passive lengthening of the muscles; but as this mechanical lengthening is about the same for all the muscles the curves retain their full value with reference to the relative change of tonus of the six muscles.

V. Reflexes on the Individual Eye Muscles (Figs. 14-21).

a. General Characteristics of the Reflexes.

The needle of the apparatus of Fig. 4 may show in addition to tonic reflexes three kinds of movements:

1. Respiratory Movements: If the blood filling of the vessels of the orbit is strong, because for some reason or other the respiration is rendered difficult, the muscles can show, if they are not well prepared, small oscillations with the rhythm of respiratory movements.

2. Slow Tonus Changes: The muscles show sometimes also during the state of rest of the animal real changes in tonus, which usually take place very slowly. For the length of the muscles must be taken the mean length between the two extreme lengths of the muscles during the oscillation.

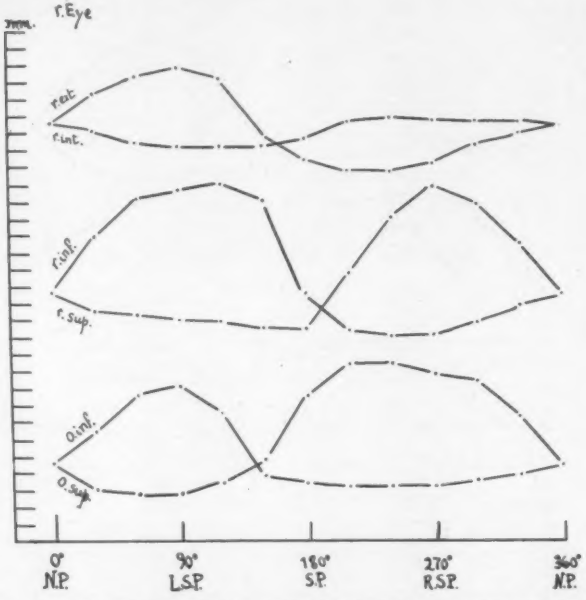


Fig. 15. The same during the longitudinal rotation; right eye; the head positions correspond to those in Figs. 11 and 13. (N. P.) normal position; (R. S. P.) right side position; (S. P.) supine position; (L. S. P.) left side position. These curves are valid for the left eye changing (R. S. P.) for (L. S. P.), and conversely.
In positions 180°-270° the increased blood filling of the orbit produces a passive lengthening of the muscles somewhat less than in Fig. 14.

It is an easy task to differentiate these tonus oscillations from the tonic reflexes: if a muscle in two consecutive head positions (for instance, in position 180° and 210° of a curve) shows such tonus oscillations of, for instance, 0.3 m.m., it will show these tonus oscillations as long as the head remains in position 180°. Then, at the transition from position 180° into position 210° it will show a

change of tonus, and then during the rest of the head again the same tonus oscillations.

Not in all rabbits are these oscillations present and also not in all head positions; usually they may be observed immediately after the preparation of the eye muscles; more seldom several hours after the operation. They are found more frequently in those head positions which should be named "not physiological."

It is easy to find an explanation of the origin of these tonus oscillations. They have never been observed in an uninjured eye. I have often attached an aluminum needle to the eye and found a "position nystagmus" in nonphysiological head positions; however, never these slow tonus oscillations. Perhaps their origin may be attributed to the lack of optical stimuli.*

3. "Position Nystagmus": In certain head positions especially in the neighborhood of the supine position, when the studied muscle ought to pass from a state of maximal relaxation into a state of maximal contraction, or conversely, there is often a strong nystagmus to be observed. In my former publications I did not determine the direction of this nystagmus quite accurately; later, however, I have recorded it and published a detailed description.† Its direction usually does not depend on the way in which the head reaches the position, in which the nystagmus appears, but one and the same muscle may, in two different head positions of the same slow rotation, produce nystagmus of opposite directions. Figs. 18, 19 and 20 show good examples.

Position nystagmus has been observed also in the intact eye. I have given (loc. cit., p. 317) the following explanation of its production:

All stimulations which regulate the tonus of the eye muscles (semicircular canals, maculae, neck nerves, opticus, etc.) must combine somewhere in the central nervous system (whether this takes place in the eye muscle nuclei or in the centers in the substantia reticularis, or elsewhere does not modify the fact); the different excitations are harmonious in physiological head positions, and no conflict is present. The nervous system, however, is not prepared for combining *not*

*Fleisch has described an optic fixation reflex of the rabbit's eye. The evidence offered by Fleisch, however, is perhaps not quite conclusive because the rabbit's eye shows a reflex of defence, which may have produced the effect described by Fleisch (Pflueger's Arch., 196, 1922).

I have described another reflex which takes place after extirpation of one eye. The rabbit shows after this operation the same symptoms which appear after extirpation of the labyrinth on the same side, although they are considerably less pronounced and, therefore, may be observed only under favorable circumstances (Trav. d. Lab. d. Rech biol., 23, 1925, Figs. 1 and 2).

†Acta Otolaryng., Vol. XI, 1927, S. 312. In this paper may be also found a description of the important experimental results of Nylen on position nystagmus. Nylen was the first to give a correct definition of position nystagmus.

harmonious stimulations as, for instance, those taking place in the neighborhood of the supine position of the head and the fight between

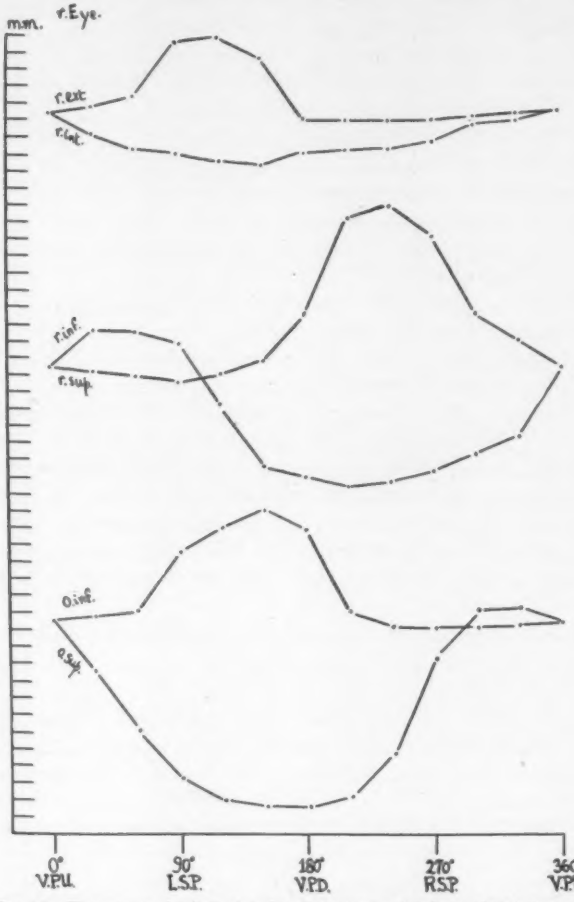


Fig. 16. The same during the dorsoventral rotation; right eye; the successive head positions are the following: Fig. 7, 90°; Fig. 13, 270°; Fig. 7, 270°; Fig. 13, 90°; Fig. 7, 90°. (V. P. U.) head vertical pointing upwards; (R. S. P.) right side position; (V. P. D.) head vertical pointing downwards; (L. S. P.) left side position. These curves are valid for the left eye changing (R. S. P.) for (L. S. P.), and conversely.

The increased blood filling of the orbit produces in the head positions, 180°-270°, a passive lengthening of the muscles almost as in Fig. 14.

partially antagonistic stimulations results in a nystagmus. This hypothesis is based on experiments in which through different opera-

tions one or more stimulations were made abnormal, and strong position nystagmus observed.

4. Dependence of the Length of the Muscles on the Direction in Which the Head Reaches a Determined Position.

If the changes in lengths of a muscle are registered in those positions of the head, which are reached during a rotation, somewhat different curves are obtained if the direction of the rotation is reversed, although the head positions are the same in both cases.

The muscles behave in the same manner as the eyes. The tonus of one muscle depends on two factors, on the position of the head

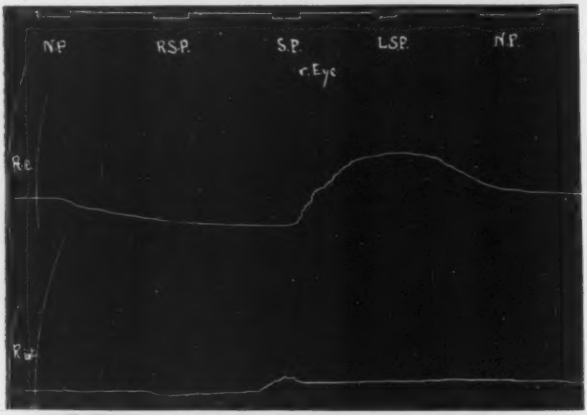


Fig. 17. Tracings of the tonic reflexes of the horizontal eye muscles during the longitudinal rotation (for the technique see Fig. 6). The positions of the head are indicated in the upper signal line, and correspond to those of Fig. 13.

In the tracings of Figs. 17-21 the blood filling of the orbit remains almost constant and therefore the control curves (tracings of paralyzed muscles or after death of the rabbit) consist of horizontal lines (see my paper in Acta Otol., 1932).

in space and on the direction in which the head is being turned before it reaches this position; consequently, one and the same muscles may be in different states of tonus in the same position of the head in space. The differences observed in physiological positions are slight, but in the nonphysiological positions they may be more pronounced.

The explanation of this dependence is not easy. Fleisch[23] speaks of a tendency of the eye to remain in the last position it had, but this only brings forth a new name for this phenomenon.

As will be seen later, the tonic reflexes, due to the centrifugal force, also depend on the direction of the rotation; the explanation

which I have given for this dependence may be also applied to the position reflexes; briefly, it consists in the following:

Position innervation depends on shape changes of the end organs of the labyrinth (membranous semicircular canals and otolithic membranes) and these changes in shape may be somewhat different in one and the same position of the head, depending on the direction in which the head has been rotated before reaching this position.

There is no doubt that this is quite correct from a mechanical point of view, but, on the other hand, physical explanations are never sufficient for biological phenomenons, as they do not take into consideration the functions of the nervous system.

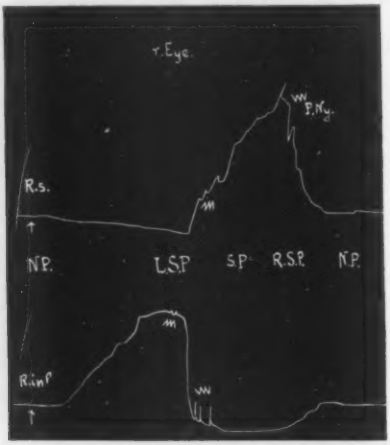


Fig. 18. Tracings of the tonic reflexes of the vertical muscles during the longitudinal rotation; the muscles show in addition to the tonic reflex in some positions of the head a position nystagmus (P. Ny.).

If the shape of the curve of a tonic reflex may change, if the head is being rotated in the opposite direction, it remains constant when the rotation is repeated in the same direction.

5. *Individual Differences:* It is interesting to mention that in the curves from different rabbits, in addition to constant features, there appear differences which sometimes are not so insignificant (see Fig. 19). I had attributed them to anatomical differences in the motor apparatus of the eyes and even tried to base the differences in the curves on certain anatomic anomalies of the eye muscles.

After having prepared many hundreds of rabbit eyes and, consequently, having accumulated numerous data on the anatomical varie-

ties of the eye muscles, I must admit that the eyes which I studied in this connection represent types which often repeat themselves. There is much work to be done in this field before we may explain the individual changes in the tonic reflexes, by anatomical differences. At present we may only say that there are present individual differences in the muscle curves as well as there are differences in the anatomy of the motor apparatus. How far these two facts can be brought into mutual dependence has to be left unsolved for the time being.

b. Curves of the Individual Muscles.

Even a superficial analysis of the curves on Figs. 14-21* allows us to draw the following conclusions:

1. All muscles participate in the production of the postural reflexes of the eye muscles.

The retractor bulbi also takes part in the producing of the tonic reflexes. My coworker, Knutson[38], could show that during the rotation of the head round the lengths axis the four parts of the retractor react in the same manner as the straight muscle lying above; these reactions are very weak. During the rotations round the bitemporal axis no reactions of the retractors could be observed.

2. It is impossible to determine theoretically from observation of the eye movements which are the muscles which produce the movement, because, although there are muscle curves similar to the curves of the eye movements, there are also quite different muscle curves.†

3. Each muscle has its own way of reacting: even muscles of the same anatomical pair may show different curves. The reactions of

*A few of the curves published by me in 1925 need slight modifications. The tracings published by me in 1927 are correct. The first ones were obtained at the beginning of my studies on the labyrinth physiology and the preparation of the eye muscles was perhaps not very good; it is possible that I did not liberate sufficiently the muscles from the surrounding tissues. In any case the differences are very slight, and only one of the conclusions stated by me in 1925 must be modified; these are not curves of tonic reflexes on the eye muscles with two points of maximum (I found then that the r. sup. and the o. inf. may show two contractions phases during a whole turn of the head and this seems to be incorrect, at least for the r. sup.). The curves for the other four muscles are correct. The curves of Figs. 14-16 have been obtained with the same technique used in 1925, but special care has been taken in preparing the eye muscles. The tracings on Figs. 17-21 were obtained in 1926-27.

†This point cannot be too strongly emphasized; special care must be taken if the reflexes after lesions in the nervous system are studied. The same movement of the eye may be brought forth by different muscle activities; for instance, horizontal eye movement backwards may be carried out by: (1) contraction of the external rectus and relaxation of the internal rectus. (2) contraction of the external rectus only, (3) relaxation of the internal rectus only, (4) simultaneous contraction of both rectus muscles if the contraction of the external rectus is the strongest (cfr. Fig. 57), (5) simultaneous relaxation of both rectus muscles if the relaxation of the internal rectus is the strongest. If no graphic methods is used the differentiation between these five cases is almost if not totally impossible. As easily seen, these five cases represent quite different kinds of innervation of the eye muscles, and all five may actually occur after lesions in the vestibularis nuclei.

the muscles of an anatomical pair are not dependent on each other according to a simple law, as, for instance, the law of reciprocal

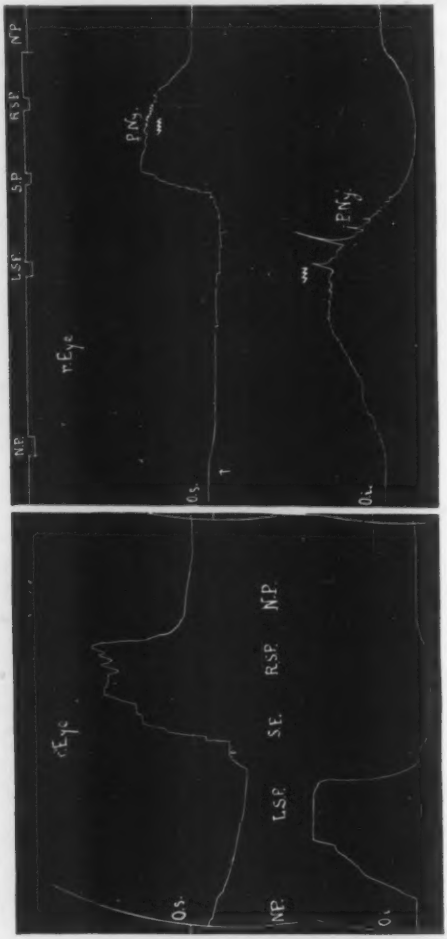


Fig. 19. Tracings of the tonic reflexes of the oblique muscles during the longitudinal rotation in two different rabbits. In both there is also a position nystagmus, stronger in the tracings on the right.

innervation. A more complicated law must be applied in this case.

4. As each muscle has its own curve of reflex, we may say that

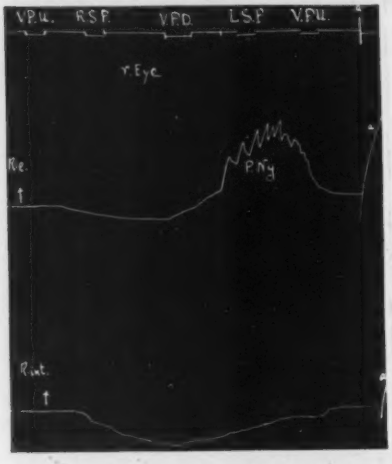


Fig. 20. Tracings of the tonic reflexes of the horizontal muscles during the dorso-ventral rotation. (V. P. U.) vertical position, muzzle upwards; (L. S. P.) left lateral position; (V. P. D.) vertical position, muzzle downwards; (R. S. P.) right lateral position (see Fig. 16).

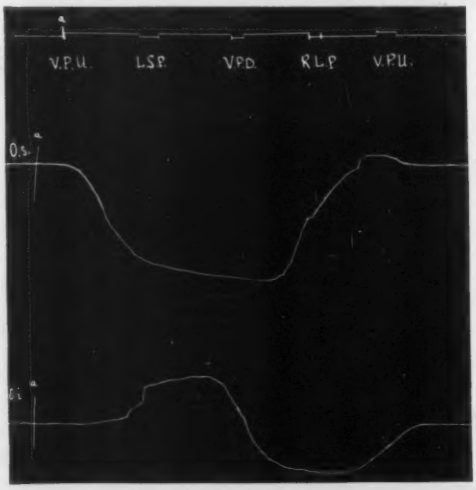


Fig. 21. Tracings of the reflexes of the oblique muscle during the dorso-ventral rotation (see Fig. 16).

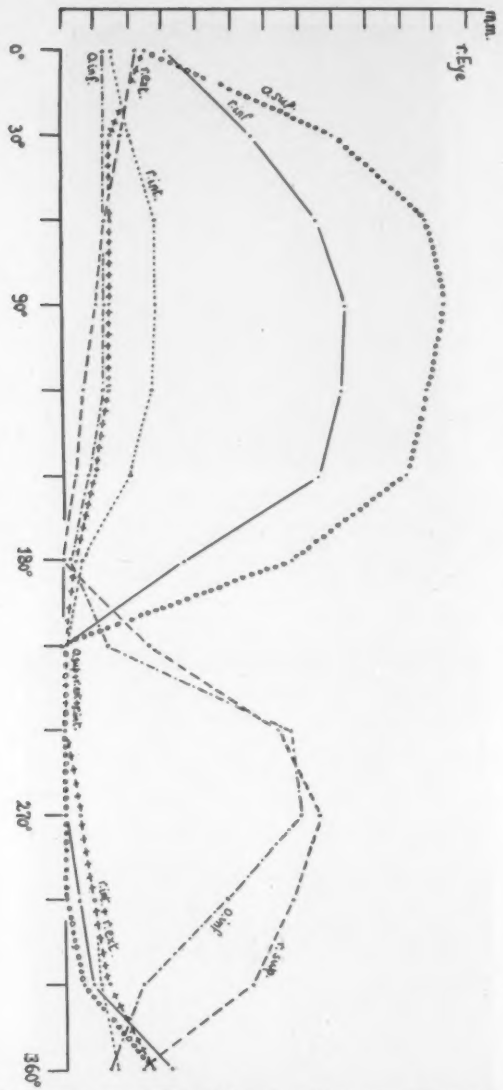


Fig. 22. The curves of Fig. 14 drawn with a common zero line in order to make an absolute comparison of the state of tonus of the six eye muscles. The zero line represents for all the muscles the length of the muscle when it shows the maximum of relaxation during the tonic reflexes; therefore the curves represent the actual isotonic shortening of the muscles under the tonic labyrinth influence. To note that the six muscles show in the normal position of the head a certain degree of contraction which is about the same for all muscles.

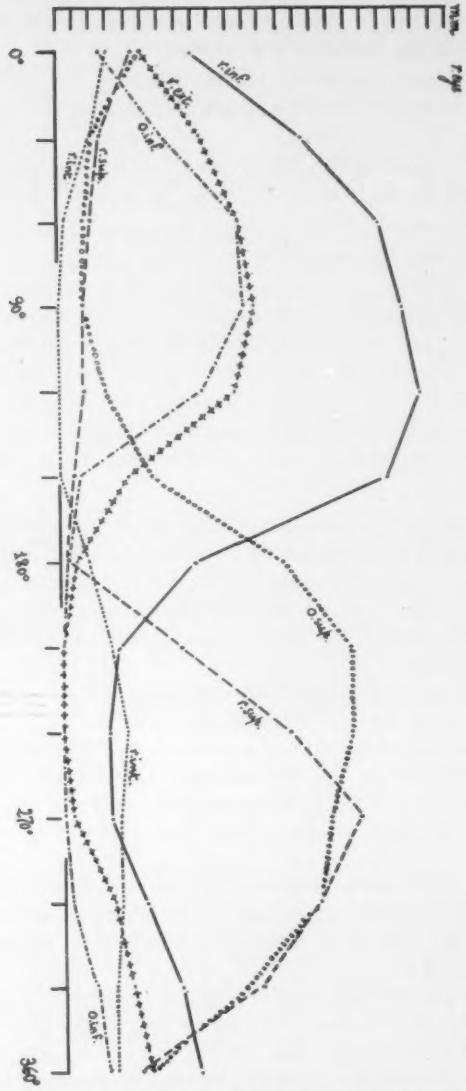


Fig. 23. The curves of Fig. 15, drawn with a common zero line.

one and the same labyrinthine innervation (*i. e.*, one and the same position innervation) causes as many reactions as there are muscles.

5. None of the curves is a sinus line.

6. Each muscle reaches its maximum contraction and maximum relaxation in definite positions which are characteristic for this particular muscle.

7. The distance between the position in which the muscle reaches its maximum contraction and maximum relaxation is less than 180°.

8. In the neighborhood of the supine position of the head, all muscles are near the relaxation maximum.

9. The transition from the contraction maximum into the relaxation maximum takes place if the head passes through the supine position in about 40°-60°, but during the passing of the head through the normal position the distance between both maximal positions is much larger.

10. The reactions of a muscle in the neighborhood of the normal head position are stronger when the muscle contracts than when it relaxes.

c. An Absolute Comparison of the Muscle Curves.

If we wish to compare the curves of individual muscles with each other, we must have a standard of comparison. In the case of eye movements we may take the tonus of the muscles during the state of rest as a standard, as the muscles start from and return into the same state of tonus.

In the case of tonic reflexes there is not a head position which we could consider as the starting point of the rotation. In our experiments we have taken the normal position of the head for the starting point, but the curves for the individual muscles would not have changed if we should have chosen any other position, only the comparison of the single muscle curves with each other would have given different results.

The sole possibility to make correct comparison is to accept that the state of the muscle, when it reaches its relaxation maximum, represents the zero line of its reaction curve, and draw all curves with the same zero line.

The zero line for each muscle may be found by comparing the curves of Figs. 14-16. The curves for all six muscles with a common zero line are reproduced in Figs. 22-24.

These curves offer us a surprise: we see that all curves in Figs. 22 and 23 have nearly common points in positions 0° and 360°; this means that *all muscles show approximately the same state of con-*

traction when the eye, in the normal position of the head in space, finds itself *in the primary position*. There is also another position of the head, in the neighborhood of the supine position, in which all muscles again have approximately the same tonus, which, however, is somewhat weaker.

These curves show that no simple law embracing all the changes of tonus of the muscles may be stated; the law can be defined only by the curves themselves. There also is no true reciprocity present in the curves of the so-called antagonistic muscles, as only short stretches of the curve of one muscle may be considered as a reflected image of that of its antagonist, because one muscle may change its tonus in a considerable way while its antagonist remains in a state of unchanged tonus, and because parts of the curves are parallel.

CHAPTER III.

Association of the Eye Muscles in Postural Reflexes.

I. Contraction of Each Eye Muscle in Different Eye Positions.

The curves on Figs. 22-24 show the state of contraction of each eye muscle in different eye positions; they, however, do not show anything definite about the strength of the forces produced by the muscles, because these depend on the size of the muscles and on the passive tension to which they are submitted. When, for instance, the r. ext. and r. int. are in the same state of contraction, the r. ext. exercises a stronger force because it is larger. The o. inf. shows in the head positions 0°-90° of Fig. 22 approximately the same state of contraction, but in the second position it exercises a stronger force, as it has been stretched by the rolling of the eye forwards.

Hering and Hoffmann have already emphasized that the most important resistance which a muscle has to overcome consists in stretching its antagonists. This statement was confirmed by Bartels, who showed that in case of nystagmus the contraction of one muscle is often stronger than the relaxation of its antagonist; we see this especially clearly in the curves for postural reflexes of the eye muscles, when the head is in the neighborhood of the normal position.

As already mentioned, Helmholtz has brought to attention the fact, that the action of one muscle in different eye positions could remain somewhat constant because the muscle insertions and bellies are wide. In rabbits there is still another factor to be taken into consideration, namely that the muscles during eye movements change their shape because the muscle bellies slide over the eye.

This may be especially clearly seen in the case of the oblique muscles. The belly of the o. sup. is shifted inwardly and outwardly during the rollings and vertical movements of the eyes. When the eye is rolled backwards or is lowered, the belly of the o. sup. will slide backwards, *i. e.*, in the direction of the equator of the eye; when the eye rolls forwards or is lifted the belly of the muscle will slide towards the cornea. The belly of the o. sup. during the rolling of the eye backwards is flat, but it takes up the shape of a thread, when the eye rolls forwards.

Similarly behaves also the o. inf.: when the eye rolls backwards the belly of the obliquus lies very near to the cornea rim and has the shape of a thread; the same happens when the eye is lowered. However, when the eye is lifted the obliquus, which changes into a wide band, slides towards the depth of the orbit.

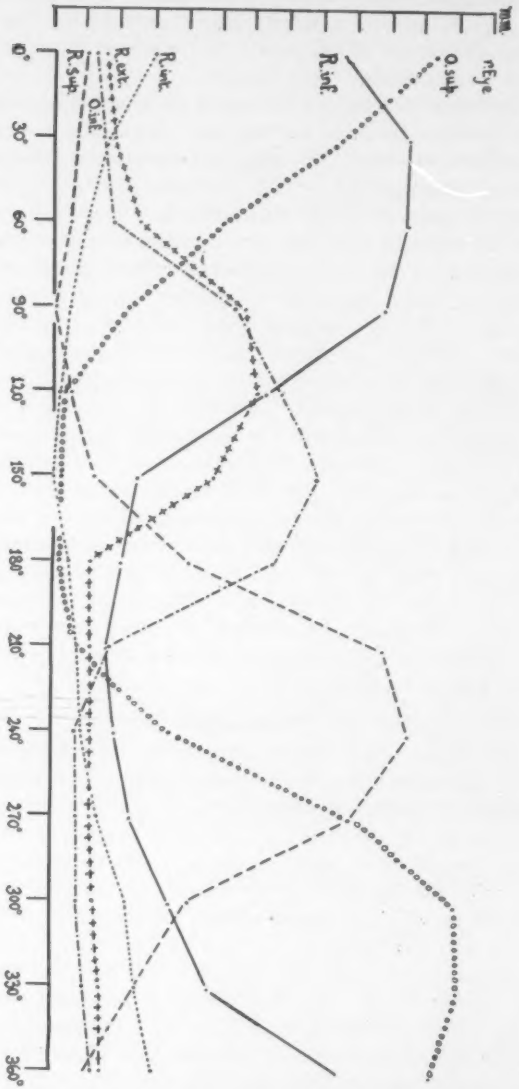


Fig. 24. The curves of Fig. 16, drawn with a common zero line. The curves of Figs. 22-24 have been obtained with the same rabbit.

In the vertical muscles it is possible also to observe similar phenomena, which may be especially clearly seen during the ab- and adductive movements of the eyes. The bellies of the muscles slide forwards and backwards over the eye.

The horizontal recti ought to behave in the same way as the vertical muscles; however, we can say nothing definite about this, as the bellies of these muscles lie too deep and therefore a direct observation is very difficult.

The experiments show that if one muscle is alone active, because the other five muscles have been cut through, its action is the same at the beginning of the contraction and when the contraction becomes maximal, *i. e.*, when the r. inf. or another muscle is active alone, the direction of the eye movement is the same at the beginning of the contraction and when it becomes maximal. On the ground of this fact we can study what happens if the eye moves in any other direction than that of the muscle. The curves of Figs. 52-54 show the muscle contractions which produce a horizontal eye movement. The vertical and oblique muscles show changes in tonus which remain constant during the whole horizontal motion of the eye. We may conclude from this that the resultant of the forces of these four muscles during the entire horizontal excursion remains constant; the action of each single muscle could have changed in each successive position of the eye—we do not know this—but if so, it was compensated by the change in the action of the other three muscles.

This confirms the validity of the theoretical assumption of Hering and Hoffmann (Chapter II, I).

II. Participation of the Vertical Eye Muscles.

The curves on Figs. 22-23 agree with the photographs on Figs. 7-13, and offer us an explanation of some of the details which we could not formerly understand.

The curves on Fig. 22 show the strong participation of the vertical muscles in the rolling of the eyes, and also that the o. inf. actually does not relax during the forward rotation of the eyes (there are even rabbits in which it shows a slight contraction). The strong contraction and relaxation of the o. sup. are clearly seen in the curves; the curves also show us that the r. int. contracts during the forward rotation of the eyes; the horizontal backward movements during the rolling backwards is produced by a simultaneous relaxation of both horizontal muscles, which may be explained by the fact that the r. ext. is stronger than the r. int.

The curves on Fig. 23 show that the r. ext. contracts strongly when the eye goes downwards and somewhat forwards and that,

consequently, in this case the r. ext. shows a strong contraction, which does not produce an eye movement.

The strong contractions and relaxations of the muscles which do not effect the actual eye deviations, for instance, the above mentioned contraction of the r. ext., cannot be explained simply by the fact that they have to correct the action of the other muscles; in the same way it is impossible to explain the lack of reciprocity in the contractions of the antagonistic muscles. An explanation is only then possible, when another condition, to which only very little attention has been given, is observed, namely the fact that the muscles must hold the rotation center of the eye.

III. The Activity of the Eye Muscles as a Fixation Mechanism of the Rotation Center of the Eye.

In fixing the position of the eye center two systems of forces are active: the pressure of the orbital tissues and the system of the

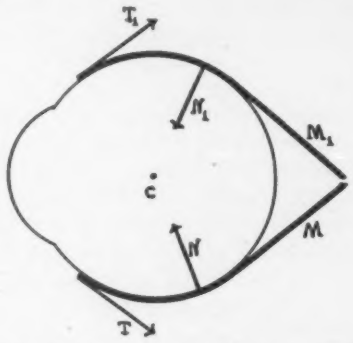


Fig. 25. Scheme showing how the muscles of the same anatomical pair may hold the rotation axis of the eye fixed in the orbit; explanation in text. This scheme corresponds very closely to the vertical eye muscles of the rabbit.

muscle forces themselves; of the two the second system is the most important, already because it regulates the first one.

The participation of the eye muscles in holding the eye rotation center may be explained in the following way:

Fig. 25 represents a schematic eye held in the initial position by means of two symmetrical muscles. The muscles M and M develop four forces: T, N, and T_1, N_1. The resultant of these four forces is compensated by the pressure of the retro-ocular tissues; the only possible deviations of the eye are straight displacements forwards or backwards, when the blood filling of the retro-ocular tissues

increases or decreases, but the eye position remains unchanged as long as the blood filling is constant.

If now muscle M contracts the eye rotates in its direction and the whole system of forces changes. The tangential force T as well as the normal force N have both increased; N has also a somewhat different direction. If muscle M_1 could be stretched without resistance the eye would be pushed out of the orbit by force N, as it actually happens when muscle M_1 has been cut through. In order to retain the rotation center in the same position in which it was before the eye was moved it is necessary that muscle M_1 exercises also stronger normal and tangential forces, which together with the corresponding forces of M will have again a resultant directed straight backwards.

Theoretically it is impossible to ascertain how muscle M_1 ought to behave in order that it should exercise a stronger force, because this muscle becomes passively lengthened during the eye movement and consequently its elasticity will even without contraction, develop an increase in force. The experiments show that this muscle usually either remains in a state of unchanged tonus or shows only a slight relaxation.

It is clear that the eye fixed in such a way can exhibit in the direction of the muscles M, M_1 only slight movements, as the forces exercised by the muscle M_1 restrict the moving ability of the eye; the motion of the eye on another axis is, however, not made difficult through the simultaneous contractions of M and M_1; if M and M_1, for instance, represents the vertical muscles, the horizontal muscles will have to overcome almost the same resistance for moving the eye in the horizontal direction as if M and M_1 were relaxed. This shows that if the two muscles have to carry out a considerable movement of the eye the fixation of the rotation center of the eye must mainly be done by the remaining four muscles; for this reason, for instance, the horizontal muscles show a true antagonistic innervation, *i. e.*, the relaxation of one muscle is nearly as strong as the contraction of the other muscle, when the eye exhibits large horizontal movements (see Chapter VII); while the vertical and oblique muscles by means of simultaneous contractions hold the rotation center of the eye.

With six nonsymmetrical eye muscles the mechanical possibilities are very numerous, and there is always present a definite combination of eye muscle contractions for each eye movement or position which holds the rotation center of the eye, without impairing the moving ability of the eyes. The curves on Figs. 22-24 give us for

each eye position the combination of muscle contractions which holds the eye in place when it is in state of rest. Later (see Chapter VII) we shall examine how these combinations change during movements of the eyes.

IV. On the Validity of the Law of Reciprocal Innervation.

If we now try to classify the eye muscles in pairs of antagonists during postural reflexes we encounter difficulties which are hard to overcome. The tonic reflexes do not represent a movement of the eye but only a mechanism used for keeping the eye in a determined position in the orbit, and during these reflexes the so-called antagonistic muscles develop forces which would act antagonistically if the eye should move, but act antagonistically in holding the eye position.

A superficial study of the curves of Figs. 22-24 would lead us to the conclusion that the law of reciprocal innervation holds true in the case of tonic reflexes; the parts of the curves for which this law seems not to be followed are really small and are only present in some muscles in nonphysiological head positions. The curves of the three pairs of muscles, as Fig. 24 shows, cannot be related to each other, because each pair of muscles reacts in a special way; moreover, the comparison of Figs. 22 and 23 shows that the three pairs combine their activities in a totally different way in the case of rotary or vertical eye motions; but both muscles of each pair are more closely related to each other than to any other muscles: the maximum and minimum head positions are the same for both, but different for each pair; on the other hand, a simultaneous contraction or relaxation of both muscles of a pair occurs very seldom and this might be explained on account of the method of recording; as a matter of fact, only perfect isometric records would be able to settle the question if really simultaneous contractions or relaxations in both muscles take place during position reflexes. So far the law of reciprocal innervation seems to hold true.

But, on the other hand, we must consider that during the third reaction (see Chapter VI) simultaneous contractions of both muscles of one pair occur very often, and that there is a capital difference between the curves of Figs. 22-24 and the tracings written by the muscles in the case of nystagmus.

In the case of nystagmus one muscle may remain in a state of unchanged tonus while its antagonist shows very strong contractions and relaxations; but the innervation is the same during the entire excursion of the eye; for instance, the r. ext. may remain relaxed while the r. int. shows strong contractions and relaxations, but then

the r. ext. remains relaxed during the entire eye movement. In the case of tonic reflexes the innervation of the muscles may change its nature during the eye displacement; for instance (see Fig. 14), if the head is rotated on the bitemporal axis between points 90°-0°-270°, the o. sup. relaxes during the entire head motion, but the o. inf. remains relaxed between 90° and 0°, and only when the head reaches the position 0°, begins to contract; *i. e.*, the rolling of the eye backwards is being brought about between points 90°-0° only through relaxation of the o. sup., and between points 0° and 270°— through relaxation of the o. sup. and contraction of the o. inf. Similar facts can be observed in Figs. 15 and 16. If we state that the

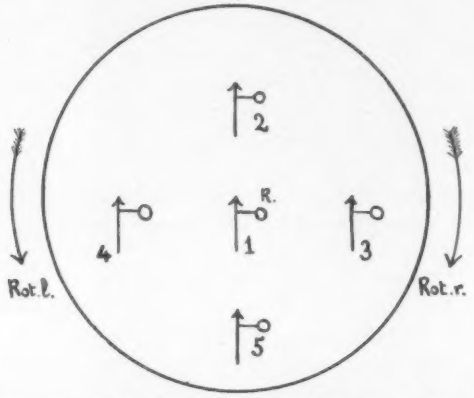


Fig. 26. The five main positions of the rabbit on the turn table in a view from above. The rabbit is represented by an arrow; the head of the arrow corresponds to the head of the rabbit. The kymograph is represented by a little circle (R) on the right side of the arrow. The two arrows (Rot. r.) and (Rot. l.) on both sides of the turn table indicate the directions of the rotation. In the case of the left eye, position 3 of this scheme is position 4, and conversely.

muscles are co-ordinated during the eye movements according to a law — we shall call it the law of reciprocal innervation — we can hardly state that the same law holds true for the position reflexes; and this difficulty is still harder to overcome if we consider that, when the change of position of the head occurs quickly and, therefore, represents a true motion, the innervation of the eye muscles changes its nature (cfr. Fig. 55, Chapter VII).

This seems to prove that the muscles follow different laws during position reflexes and motion reflexes, an assumption supported by the fact that both kinds of reflexes are regulated by partly different cen-

ters in the medulla; for instance, the destruction of the triangular nucleus at the floor of the fourth ventricle inhibits tonic reflexes without preventing the appearance of nystagmus[47, p. 76; 50, p. 218].

The law of reciprocal innervation, as Sherrington and Bartels stated it, and as de Kleyn and Magnus claim to have proved it, does not hold true in the case of tonic reflexes; de Kleyn and Magnus state that one muscle relaxes when its antagonist contracts and therefore the curve of one muscle must be a reflection of the curve of its antagonist. De Kleyn and Dusser de Barenne have recently confirmed my statement that this law does not hold true. Another question raised by de Kleyn and D. de Barenne is whether or not the law of reciprocal innervation, as I have modified it[46, p. 301] (see Chapter VI), holds true in the case of tonic reflexes. I do not think so, because sometimes simultaneous contractions or relaxations of both antagonistic muscles take place, but even if these simultaneous contractions were due to defects in the recording method, we ought to state that the co-ordination of antagonistic muscles in the case of nystagmus and in the case of tonic reflexes is of different nature, although both muscles of an antagonistic pair during nystagmus, as well as during tonic reflexes, are more closely bound to each other than to any other muscle. Much research work in this line has to be done before we can reduce all the features of reflexes to simple laws and I am of the opinion that it is best to wait for future discoveries before we make any definite statements. That both muscles of one pair may show very strong simultaneous contractions in the case of the third reaction lies beyond any doubt (see Chapter VI); in the case of the corneal reflex simultaneous contractions of all the four straight muscles were recorded in 1927[47] (see, too, Chapter VIII).

CHAPTER IV.

Regulation of the Eye Position During Rotations With Constant Speed.

I. Technique for Recording the Rotation Reflexes on the Eye Muscles.

The rotation reflexes on eye muscles have been registered by means of Bartel's technique.

The rabbit board and the kymograph are placed on a 2 m. x. 60 c.m. table, which can rotate round the vertical axis by its center; the eye muscles are attached by pairs to writing levers[44, 45]. The head of the rabbit is kept in place by means of a Czermak clamp, so that even the slightest movement is impossible. The body and limbs are also made immovable by binding them with cotton and bandages to the board. The rabbit board, the lever holder and the kymograph are screwed to the turn table; in addition to this the lever holder is tightened with three steel wires in order to insure its rigidity against the centrifugal force. The very light and well equilibrated levers are arranged in the lever holder in such a manner that their axes coincide with the rotation radius; this simple measure is sufficient to prevent mechanical changes resulting from movements of the turn table. Repeated control experiments showed that when the muscles should not produce any reflexes or if they were damaged, the tracing made by the lever consisted of a horizontal line. The condition of the apparatus was checked very often during the experiments in order to have absolute security that the following conditions were always present:

1. Any muscle contraction appears in the tracing.

2. No other changes, during or after rotation, except those brought about by the contraction or relaxation of the muscles, find place in the tracings.

The turn table was rotated with constant speed by means of an electric motor; as the latter, however, proved too weak to set the table in motion, I have started the motion of the table by hand and stopped it after rotation in the same way. With certain practice it was possible to reach an almost constant acceleration at the beginning and at the end of the rotation. The animal was placed on the turn table in different positions and was rotated with the head in different positions in space. Usually the muscles of the right eye were studied.

The positions of the animal on the turn table are represented in Fig. 26 and the positions of the head in Figs. 7 and 11.

II. Tonic Reflexes Resulting from the Action of Centrifugal Force.

Movements in a straight line with constant speed do not bring about any labyrinthine innervation, as the labyrinth reacts only to acceleration. During such movements only optic reflexes can be elicited (so-called railroad or optic nystagmus), of which there will be no mention here as the rabbit does not show optic reflexes. Accelerated movements in a straight line, however, bring about reflexes, which were described by Fleisch[24].

Rotations with constant speed do not produce any reflexes when the rotation axis passes between both ears. But in case of eccentric

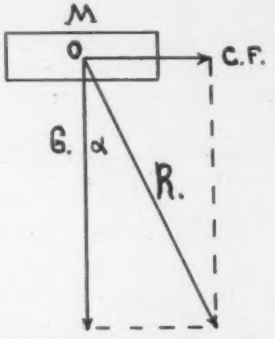


Fig. 27. Scheme to explain the action of the centrifugal force upon the labyrinth. (G) gravity; (C. F.) centrifugal force; (R) the resultant of both; to note that (R) has a different direction and also a different absolute value than (G); (∝) the angle of the apparent inclination of the head.

rotations maintained with constant speed, the centrifugal force brings forth some reflexes. Their existence was already presumed by Mach[51], who already knew of the sensations caused by the centrifugal force. Kreidl[39] and Breuer and Kreidl[16] thought it very probable that the centrifugal force produces tonic reflexes on the eyes. But a systematic experimental study of these reflexes during rotations with constant speed and the proof that these reflexes are actually produced by the centrifugal force were given for the first time by me[45]. In another paper[50] I have given a short description of the main features of these reflexes; here I shall only give a comparison of them with the position reflexes.

The origin of tonic reflexes caused by the centrifugal force is clearly demonstrated in Fig. 27. During the rotation two forces influence the labyrinth: the centrifugal force and gravity; both have a resultant, the direction of which is, of course, not vertical. The apparent, as well as the actual, inclination of the head brings about a change in the position of the eyes. With different speeds and rotation radiuses (rotation radius = distance of the head from the center of the turn table) used by me, the centrifugal force caused an inclination of the head of from 10° to 58°, usually, however, approximately 30°. Consequently the labyrinth undergoes the same stimulus as if the head was actually inclined. We shall call this inclination the "apparent" inclination of the head in opposition to the actual inclination. The apparent inclination lasts as long as the speed of the rotation remains constant. Changing the position of the animal on the turn table and the position of the head in space, it is possible to produce any apparent inclination of the head and, consequently, check all the sections of the curves reproduced on Figs. 22-24. It is necessary, however, to take into consideration the following features of the tonic labyrinthine reflexes produced by the centrifugal force:

a. The tonic labyrinthine reflexes brought about by the centrifugal force may appear somewhat different during a rotation to the right. or to the left.

b. They may be also somewhat different if the rotation is started slowly or quickly.

As easily seen, these two sentences state nothing else except that also in the case of tonic reflexes produced by the centrifugal force the tonus of the muscles depends on the manner in which the head reaches the apparent new position. Usually it is only a matter of small quantitative differences in contraction or relaxation, and only as an exception may a qualitative difference (contraction instead of relaxation and conversely) be observed.

c. The tonic reflexes caused by the centrifugal force are determined by two factors: *1*. the apparent inclination of the head; and *2*. the increase of the absolute value of the force of gravity; therefore, the reflexes represent a mixture of position reflexes and reflexes due to a progressive acceleration; the modification of the tonic reflexes caused by this second factor is usually small, and requires a special study to be demonstrated.

I shall now give some examples which serve as control of the curves of Figs. 22-24.

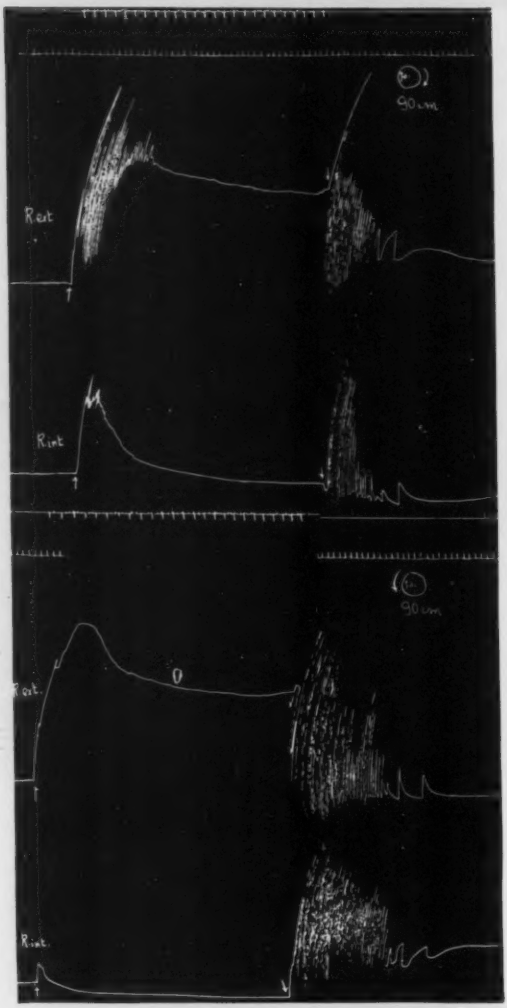


Fig. 28. Reactions of the horizontal muscles to rotations, to the right (upper curves) and to the left (lower curves). Muscles of the right eye. The upper signal indicates the rotations of the table, the lower one the time in seconds. (r. ext.) external rectus; (r. int.) external rectus. Shifting of the tracing indicates contraction of the muscle. The beginning of the rotation is indicated on the tracing with upwards pointing arrows, the end with downwards pointing ones.

Upper curves: the (r. ext.) shows at the beginning of the rotation a strong nystagmus, during the rotation a strong tonic contraction due to the action of the centrifugal force. At the end of the rotation a strong nystagmus appears. The (r. int.) shows nystagmus but no tonic reflex.

To note that both muscles show a simultaneous increase in tonus during the nystagmus at the beginning of the rotation. In the lower curves the r. int. shows a tonic relaxation during the rotation; at the beginning of the rotation no nystagmus appears (for the explanation, see my former papers[50]).

The position of the rabbit on the turn table is indicated at the top of the figure (Pos. 4, Fig. 26); the head finds itself in the normal position 90 c.m. away from the axis. The centrifugal force produces an apparent inclination of the head towards the left lateral position; this inclination corresponds to the curves on Fig. 23, between the head position 0° and 60°.

1. ROTATIONS WITH THE HEAD IN THE NORMAL POSITION IN SPACE.

Complete tracings were already given in my previous publications. Concerning the horizontal muscles it is

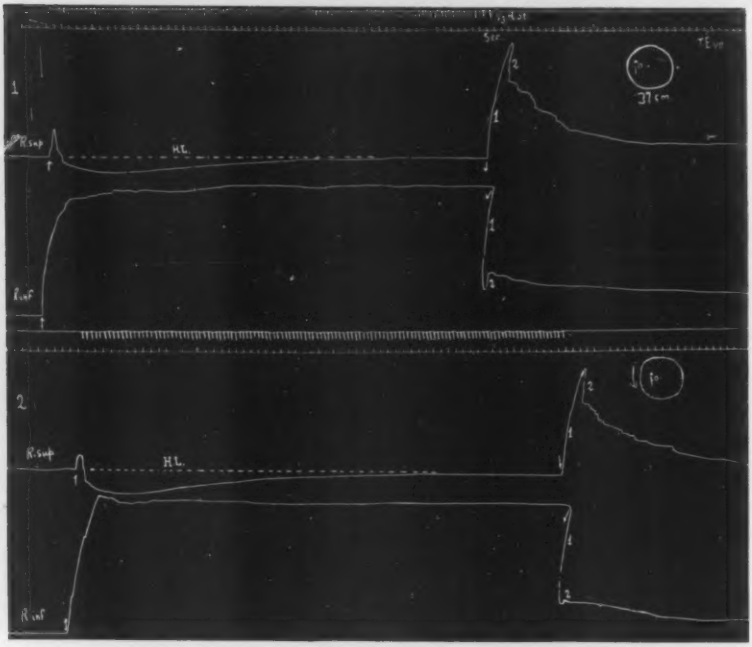


Fig. 29. Reactions of the vertical muscles to rotations under the same conditions as in Fig. 28; the upper signal gives one-third rotation of the turn table; the head was placed only 37 c.m. away from the rotation axis.

Upper curves: rotation to the right. At the beginning of the rotation indicated by the upward pointing arrow, both muscles contract (third reaction to the rotation); during the rotation the r. inf. shows a tonic contraction (tonic reflex to the centrifugal force); at the end of the rotation a third reaction to the rotation appears quite different from the reaction at the beginning of the rotation; the muscles show first a phasic reflex (1, 2), during which the muscles are reciprocally innervated and then both muscles remain slightly contracted during several seconds.

Lower curves: rotation to the left.

In both groups of curves the muscles show at the end of the rotation, in addition to the third reaction, a small nystagmus.

The apparent inclination of the head due to the centrifugal force corresponds to the segments 0°-30° of the curves on Fig. 23.

not easy to demonstrate the tonic reflexes during rotations where nystagmus is strong. Only in the case when the tonic reflex is also very strong can we recognize it without doubt. This takes place, for instance, when the head shows an apparent inclination towards the

side position, with the studied eye above. The r. ext. should produce, according to Fig. 22, a strong tonic contraction. We actually find it in Fig. 28. The r. int. remains in one case unchanged and in the other shows a slight relaxation.

If we compare the tracing of the r. ext. in Fig. 28 with that of the r. inf. on Fig. 29, we see that both muscles during the rotation

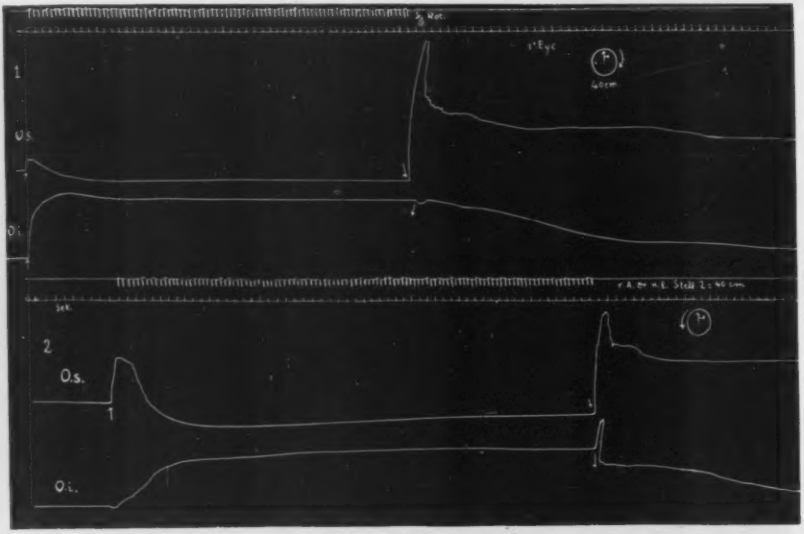


Fig. 30. Reactions of the oblique muscles to rotations. Head in the normal position in space. The position of the rabbit on the turn table is indicated on top of the figure (Pos. 2, Fig. 26), the distance of the head from the axis was 40 c.m.

Upper curves: Rotation to the right. At the beginning of the rotation both muscles show a sudden contraction (third reaction) during the rotation the superior obliquus relaxes and the inferior obliquus contracts (tonic reflexes due to the centrifugal force), at the end of the rotation the muscles show first a phasic reaction, with reciprocal innervation, and then an increase in tonus, which lasts as long as the horizontal muscles show nystagmus.

Lower curves: Rotation to the left. The tonic reflexes due to the centrifugal force are the same as before, but the third reaction is different.

The apparent inclinations of the head due to the centrifugal force correspond to the segment 360°-330° of the curves in Fig. 22.

show approximately equally strong contractions; in the case of an inclination of the head, however, the contraction of the r. inf. is stronger (see Fig. 23). We must therefore accept that the increase in the contraction of the r. ext. during the rotation depends on the increase of the absolute value of the acceleration acting on the labyrinth.

For the reflexes of the vertical muscles I wish to refer the reader to my former publications.

The oblique muscles show reflexes which correspond to the tracings on Figs. 22-24.

The o. sup. must contract if the head goes into the position head vertical, muzzle pointing upwards (see Fig. 22), or into the lateral position with the studied eye underneath (see Fig. 23); it must relax if the head goes into the position head vertical, muzzle down-

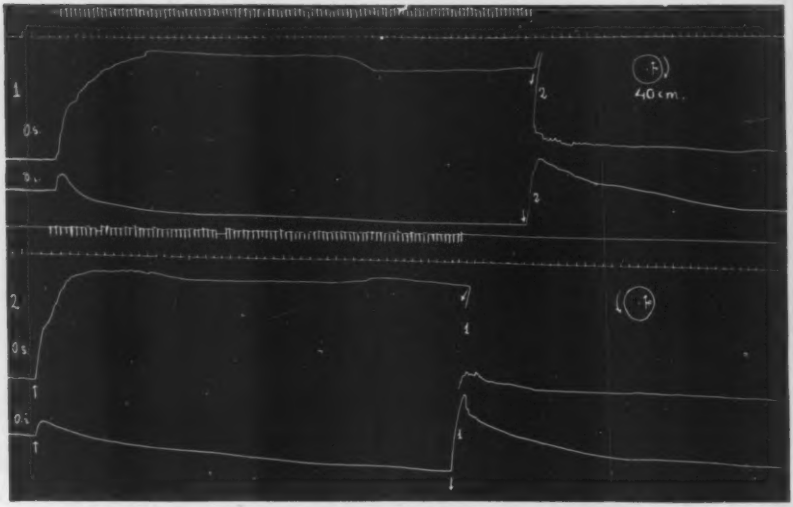


Fig. 31. Reactions of the oblique muscles to rotations. Head in the normal position; rabbit in position 3 of Fig. 26; distance of the head from the axis, 40 c.m. The tonic reflexes due to the centrifugal force correspond to the reflexes in Fig. 23, 360°-330°. The third reaction at the beginning of the rotation is the same in both cases (upper curves—rotation to the right, lower curves—rotation to the left), but at the end of the rotation it is quite different in its first phasic part.

wards (see Fig. 22), or into the lateral position with the studied eye underneath (see Fig. 23). These are actually the reflexes which are to be found in Figs. 30-33.

The o. inf. must contract when the head is inclined towards the lateral position with the studied eye above (see Fig. 23), or the position head vertical, muzzle downwards (see Fig. 22); it must relax when the head is inclined towards the lateral position with the studied eye underneath (see Fig. 23). These reflexes are actually present in Figs. 30-32.

The curves on Fig. 22 demonstrate that the o. inf. should not show any considerable change in its tonus during the passing of the head from the normal position into the position head vertical, muzzle upwards. In some rabbits, however, a slight contraction may occur, although generally a weak relaxation appears or no change in tonus at all. In the tracings reproduced on Fig. 33, we find in the upper tracing a weak contraction and in the lower one a weak relaxation. In this rabbit the o. inf. remained probably unchanged during the actual change in the position of the head.

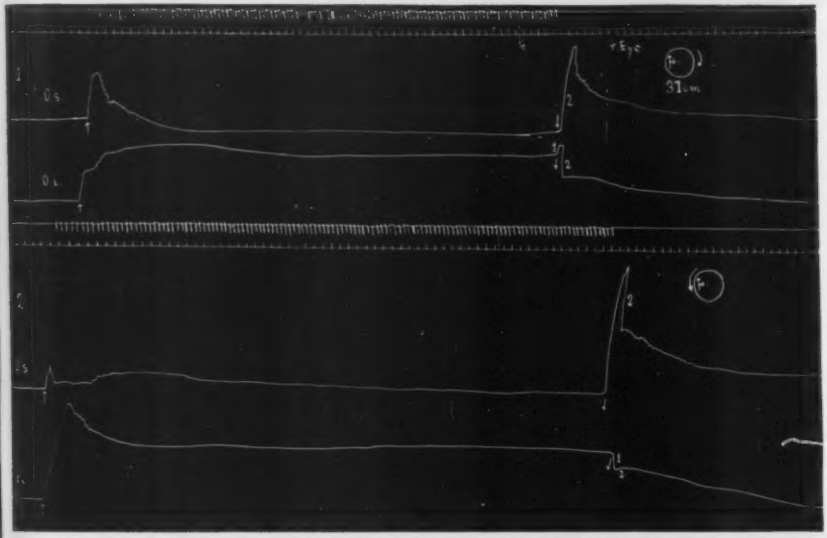


Fig. 32. Reactions of the oblique muscles to rotations; head in the normal position, 40 c.m. away from the axis; rabbit in position 4 of Fig. 26. The tonic reflexes due to the centrifugal force correspond to the reflexes in Fig. 23, 0°-30°. Upper curves—rotation to the right, lower curves—rotation to the left. The third reaction at the beginning and at the end of the rotation is different in both cases. The numerals (1, 2) on the curve at the end of the rotation give the succession of the contractions in both antagonistic muscles during the first (phasic) part of the third reaction.

As an example that the o. inf. contracts in some rabbits, I give the tracings of Figs. 34 and 35.

The tracings of Fig. 34 represent reflexes during rotation to the right; the distance of the head from the axis being about 10 c.m. in the upper tracing and 40 c.m. in the lower one; the reflexes are stronger in this last one. The head was not in the normal position in space, but inclined some 35° upwards round the bitemporal axis.

i. e., approximately in the position, 35°, of Fig. 7. The centrifugal force brought about an apparent inclination of the head towards the normal position.

Both muscles—the o. sup. and the o. inf.—showed a tonic relaxation, weaker in the case of the o. inf. This means that both muscles would have contracted during the passing of the head from the normal position into the 35° position.

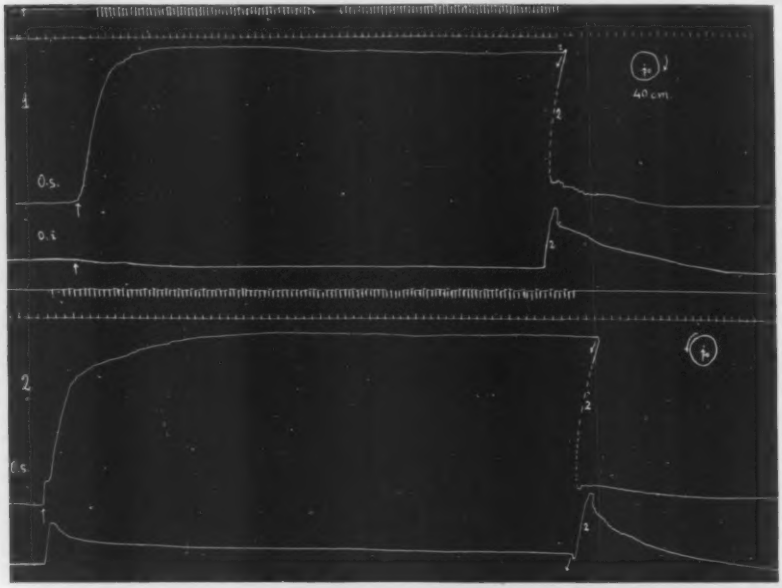


Fig. 33. Reactions of the oblique muscles to rotations; head in the normal position, 40 c.m. away from the axis; the rabbit in position 5 of Fig. 26. The tonic reflexes due to the centrifugal force correspond to the segment 0°-30° of Fig. 22. The contraction of o. sup. is very strong in both cases. The o. inf. in the upper curve (rotation to the right) shows a slight relaxation, in the lower one (rotation to the left) a slight contraction, which, however, may be due to a modification of the tonic reflex through the foregone third reaction.

The third reaction at the beginning of the rotation is different in both cases, but it is very similar at the end of the rotation.

If we compare the third reactions in Figs. 31-33, we find that there is no dependence of the direction of the third reaction on the direction of the rotation, as sometimes these reactions had the same directions at the end of a rotation to the right and at the end of a rotation to the left; on the other hand, the dependence on the position of the rabbit on the turn table is very clear.

The relaxation of both muscles may be still better observed in Fig. 35, where the rotation was started and stopped with slow acceleration and consequently there was present only a very weak rotation reaction.

When the head was then brought into the normal position in space and the rotation repeated, the o. sup. still showed a relaxation, but the o. inf. showed a contraction, as in Fig. 30; in this case the apparent change in the position of the head occurred between the positions 360°-330° of Figs. 7 and 22.

2. Rotations With the Head Vertical, Muzzle Downwards.

Fig. 36 shows reactions of the vertical muscles. The distance of the head from the rotation axis was about 40 c.m., and the centrifu-

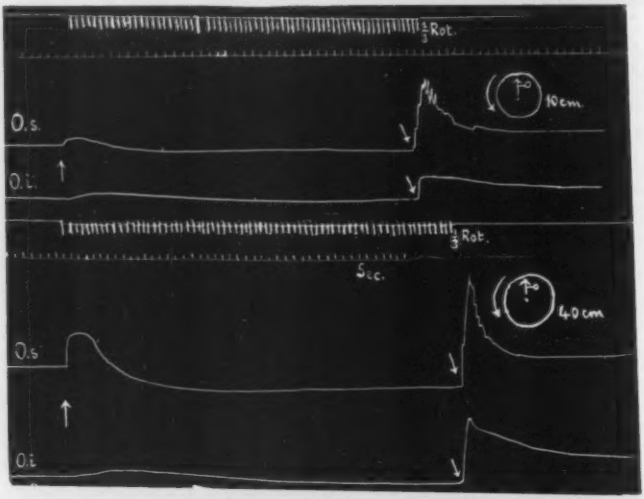


Fig. 34. Reactions of the oblique muscles to rotations; head horizontal (about 35° of Figs. 7 and 22); rabbit in position 2 of Fig. 26. Rotations to the left. In the upper curves the distance of the head from the axis was 10 c.m.; in the lower ones, 40 c.m. Upper signal one-third of rotation, lower one time in sec.

The tonic reflexes due to the centrifugal force correspond approximately to the segments 35°-25° and 35°-5° of Fig. 22. At the beginning of the rotation both muscles show a third reaction similar to that in Fig. 30. During the rotation both muscles show a tonic relaxation due to the centrifugal force, stronger in the lower curves. (Compare with Fig. 30, where the apparent inclination was between points 360°-330° of Fig. 24 and the inferior obliquus showed a contraction.)

gal force brought about an apparent inclination of the head towards the right lateral position.

In the curves on Fig. 24 we see that the r. inf., when there is an actual inclination of the head, shows a slight relaxation and the r. sup. a contraction. In Fig. 36 we find exactly these reflexes.

3. Rotations With the Head in the Supine Position.

In Fig. 37 we reproduced tracings of the reflexes of the horizontal muscles. The head was held in the supine position with the

Fig. 35. The same as in Fig. 34; the rotation to the right is started with a small acceleration in order to avoid the third reaction, but the speed of the rotation in the middle part of the curve is the same as before. The upwards pointing arrows show the beginning of the rotation, the downwards pointing ones the moment where the speed of the rotation diminished. The tonic relaxation of both muscles, in the parts of the curves between (* *) signs where the rotation speed was constant, is very clear.

external semicircular canal lying horizontally in space; the distance of the head from the rotation axis was 40 c.m. The centrifugal force brought about an apparent inclination of the head of about 30° towards the right lateral position, which, according to Fig. 23, should produce a contraction of the r. int. and a relaxation of the r. ext. The relaxation of the r. ext. can be well observed in Fig. 38; the contraction of the r. int. did not take place.

4. Rotations With the Head in the Left Lateral Position. During the passing of the head from the left lateral position into the position head vertical, muzzle downwards, the r. ext. must re-

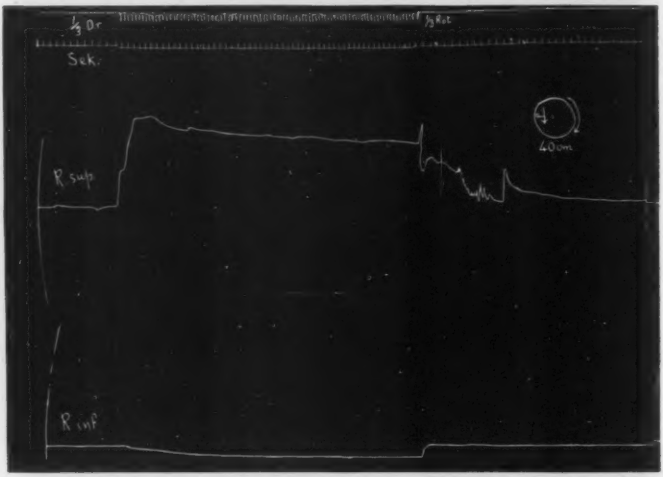


Fig. 36. Reactions of the vertical muscles to rotation; head in position 300° of Figs. 7 and 22. Rabbit in position 3 of Fig. 26. Distance of the head from the axis, 40 c.m. The apparent inclination of the head due to the centrifugal force corresponds approximately to the segment 180°-270° of Fig. 24. The r. sup. shows a strong contraction, the r. inf. a slight relaxation.

main unchanged and the r. int. must relax (see Fig. 24). In Fig. 38 we find these reactions.

If the head starting from the above mentioned position is inclined towards the supine position (see Fig. 23) or towards the position head vertical, muzzle downwards (see Fig. 24), or towards the position held vertical, muzzle upwards (see Fig. 24), the r. sup. must show almost no change in its tonus. R. inf. should relax when the head passes into position head vertical, muzzle downwards (see Fig. 24), but it should contract when the head is inclined towards the position head vertical, muzzle upwards (see Fig. 24), or in the

Fig. 37. Reactions of the horizontal muscles to rotations. Head in the supine position (position 180° of Figs. 7 and 13); rabbit in position 3 of Fig. 26. Distance of the head from the axis, 40 c.m. Curves on the left—rotation to the right quickly started and stopped; curves on the right—rotation to the left slowly started and stopped. At the beginning of the rotation to the right only a weak nystagmus appears, whereas at the end of the rotation the nystagmus is strong. In the curves of the rotation to the left the nystagmus at the beginning and at the end of the rotation is almost equally strong (at the beginning chiefly due to the r. int., at the end to the r. ext.). These curves show the difference between quickly and slowly started rotations (S. Ergebn. d. Physiol., 32, 1931, Fig. 33, p. 135).

The apparent inclination of the head due to the centrifugal force corresponds approximately to the segment 180°-150° of Fig. 23; r. ext. shows therefore a tonic relaxation.

supine position (see Fig. 23). These are the reflexes which we observe in Figs. 39-41.

It is necessary to point out here again that the reflexes are not being brought about only by the apparent change in the position of the head, because this explains that the r. inf., which has almost reached the maximum of its postural tonus in the lateral position,

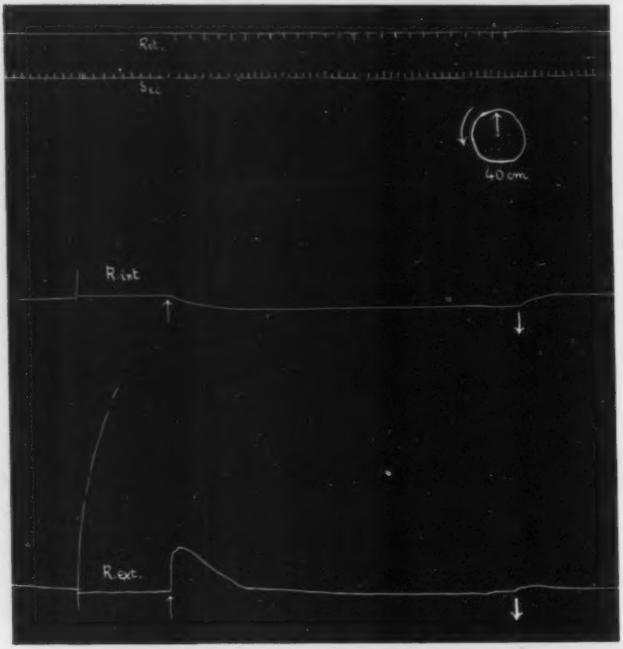


Fig. 38. Reactions of the horizontal muscles to a rotation to the right. Head in the left lateral position (90°, Figs. 13 and 23). During the rotation the r. int. showed a tonic relaxation, the r. ext. remained unchanged (90°-120°, Fig. 24). To note that neither at the beginning nor at the end of the rotation nystagmus appeared, although the nystagums was very strong when the head during the rotation was placed in the normal position, and it was strong, too, when the head was placed in the position 90° of Fig. 7 (modification of the motion reflexes due to position reflexes).

shows during the rotation, owing to the influence of the centrifugal force, still a strong contraction.

From this we may draw another conclusion, namely that the muscles during the position reflexes do not reach the maximal contraction of which they are able. But, on the other hand, it must be

pointed out that I never observed a further relaxation of a muscle when, owing to the position of the head in space, it already showed the maximum of relaxation.

Summarizing the described facts, we may state that during rotations with constant speed round the vertical axis the centrifugal force brings about certain reflexes on the eye muscles, which are

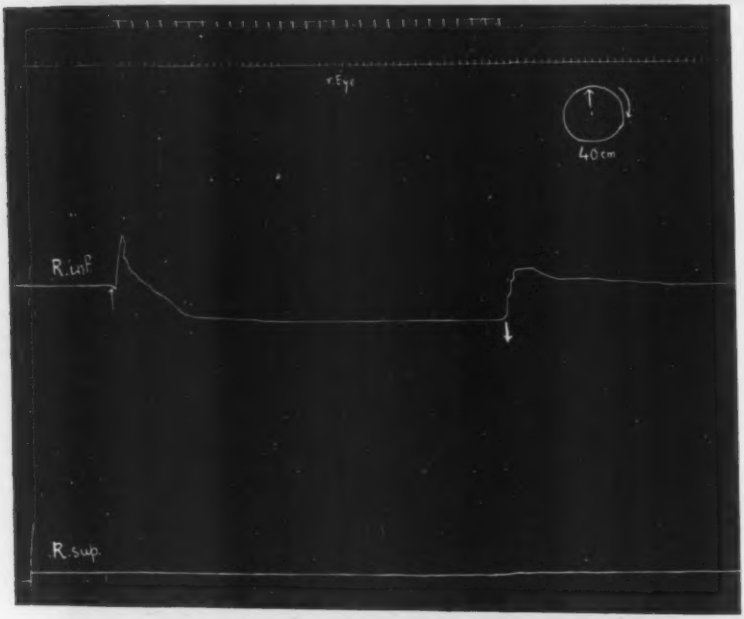


Fig. 39. Reactions of the vertical muscles to a rotation to the right. Head in the left lateral position; the rabbit in position 2 of Fig. 26. During the rotation the centrifugal force produces an apparent inclination of the head towards the position head vertical, muzzle downwards (90°-120°, Fig. 24), therefore the r. inf. shows a strong relaxation and the r. sup. no change in tonus.

very similar to the tonic position reflexes. The co-ordination of the muscles seems to depend on the same laws as in the case of position reflexes. Between the position reflexes and the reflexes due to the centrifugal force there are some differences due to the fact that the resultant of gravity and centrifugal force has a greater absolute value than gravity itself.

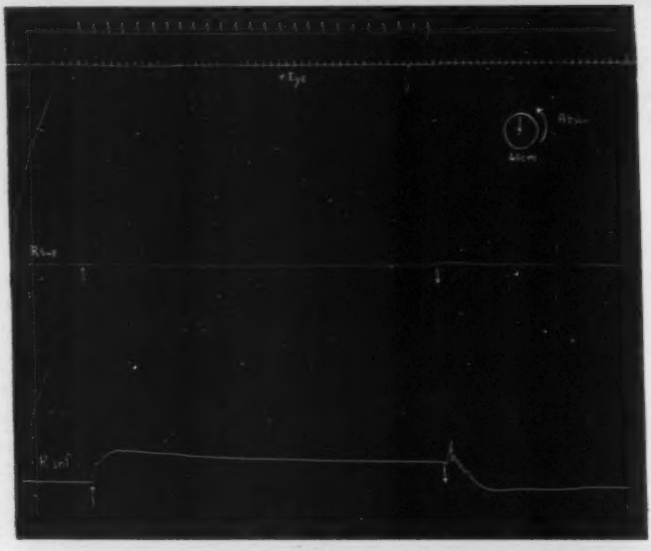


Fig. 40. Reactions of the vertical muscles to a rotation to the left. Head in the left side position; the rabbit in position 5 of Fig. 26. The centrifugal force produces an apparent inclination of the head towards the position head vertical, muzzle upwards (90°-60°, Fig. 24), therefore the r. inf. shows a tonic contraction during the rotation, the r. sup. does not change its tonus.

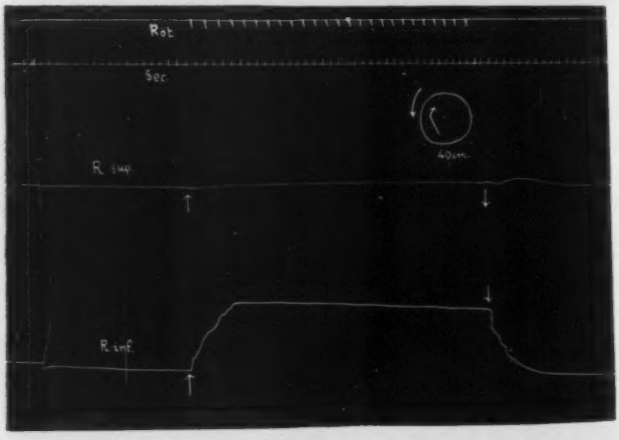


Fig. 41. Reactions of the vertical muscles to a rotation to the left. Head in the left side position, the rabbit in position indicated at the top of the figure. The centrifugal force produces an apparent inclination of the head towards the supine position (90°-120°, Fig. 23). The r. inf. shows a strong tonic contraction. The contraction of the r. inf. on account of the increase of the absolute value of the acceleration acting on the labyrinth (Fig. 27) is much stronger than that in the case of an actual inclination of the head.

CHAPTER V.

Rotation Reflexes on the Eye Muscles.

I. Reflexes Produced by Rotations on a Vertical Axis.

Rotation brings forth a reflex reaction in the eye which has been called nystagmus. The nystagmus has two phases—a slow one in the direction opposite to that of the rotation and a quick one, in the same direction as the rotation. If the rotation acceleration, although above threshold, is small, the quick phase of the nystagmus can be absent. In this case the nystagmus consists only of a deviation of the eyes. Bartels[10] has published curves of rotation reactions consisting only of the slow phase, when the animal was either anesthetized or when the rotation acceleration was very small. Also myself and recently Undritz[66] have published such curves. I have described in detail the mechanism of the production of the quick phase in another paper[47, 50].

The law which regulates the direction of the sensations during and after rotations, was already correctly determined by Purkinje. Breuer, Ewald and Bárány* have issued a simple law concerning the direction of the nystagmus: "The eye nystagmus occurs in the rotation plane and has the opposite direction of the lymph currents in an ideal semicircular canal also lying in the rotation plane."*

There is no doubt that this rule is in many instances true; there are, however, cases when it cannot be applied.

Some years ago[45, p. 289; 50] I showed that the direction of the nystagmus in the muscles is not necessarily dependent on the direction of the lymph current because two lymph currents of opposite direction can bring forth the same kind of nystagmus and one and the same lymph current can give rise to nystagmus in both opposite directions. The position of the head in space, in which the lymph current is produced plays a very important role and together with the lymph current determines the direction of the nystagmus (see Figs. 42 and 45).

In the case of eye nystagmus it is in many instances very difficult to ascertain if the foregoing rule is applicable or not, because the eye movements are of a very complicated nature. I shall not deal extensively with this subject, because complete experiments are not yet available, but I should like to bring this problem to the reader's attention, by mentioning just a few facts.

*The reader will find a complete exposition of the problem of nystagmus in the following papers: Breuer[14, 15], Barany[1, 2], Buys[17], Fischer[21], Grahe[26].

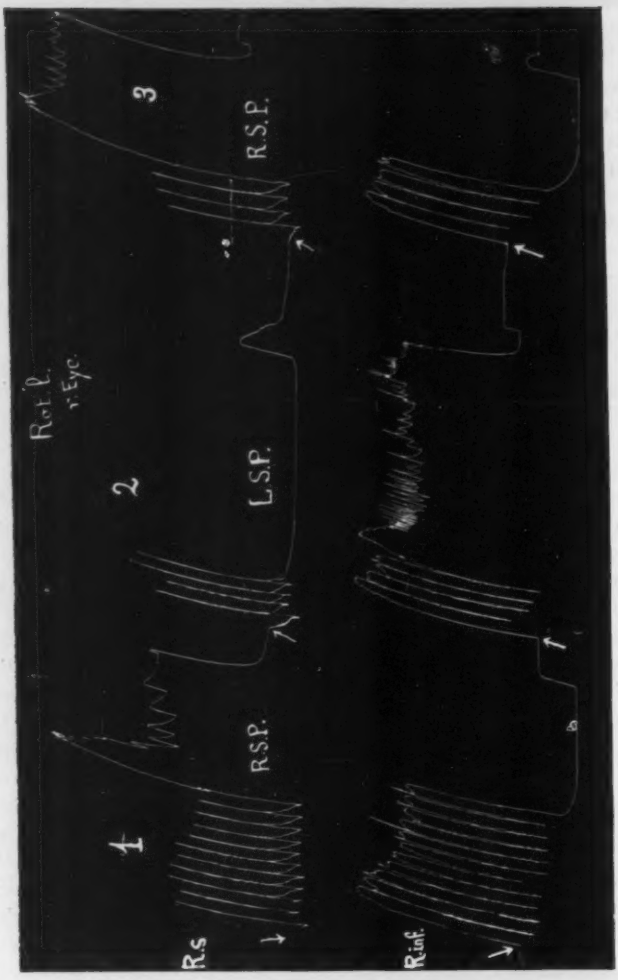


Fig. 42. Reactions of the vertical muscles to rotations to the left on the horizontal axis (longitudinal rotation, Figs. 6 and 13) right eye.

1. The rotation starts from the normal position in space, and consists of eleven turns to the left. At the end of the rotation the head remains in the right side position, the superior rectus shows a nystagmus with contraction as a quick phase; this nystagmus corresponds to a vertical eye nystagmus upwards.

2. Three turns to the left; at the end of the rotation the head remains in the left side position, the inferior rectus shows a nystagmus with contraction as a quick phase, which corresponds to a vertical eye nystagmus downwards.

3. Three turns to the left; at the end of the rotation the head remains again in the right side position; the r. sup. shows the same nystagmus as in 1.

The same rotation to the left produces an opposite nystagmus, depending on the position of the head in space at the end of the rotation.

The oblique muscles showed the same kind of nystagmus as the vertical ones, but the horizontal muscles had always nystagmus in the direction indicated in the tables of Fig. 44.

Bartels long ago pointed out that in rabbits the eye movements during nystagmus may be very complicated; he attached to the eye a straw and observed that the eye movements during the rotation show not only a horizontal component, but also vertical and rotary ones. From the illustrations in Bartels publications, however, it may be seen that he made use of eccentric rotations, during which, as already mentioned (see Chapter IV), reflexes are brought forth by the centrifugal force and also the third reaction (see later) appears.

I have conducted a systematic experimental examination of the reflexes in the muscles, but I was not able to study the eye movements, for lack of the necessary equipment; only in special cases was I able to obtain tracings of them[44]. Fig. 43 reproduces curves of the horizontal and vertical components of the eye movements during an eccentric rotation, but it is not possible to give a definition of the eye movements on the ground of these curves, because the rotary component was not recorded. In any case it may be concluded with absolute certitude, that during these kind of rotations the eye movements do not take place in the rotation plane, undoubtedly because the apparent changes in position which appear during the rotation are compensated by vertical and rotary motions of the eye.

In the case of centric rotations, under quite definite conditions, the nystagmus occurs in the rotation plane. If the head lies in the normal position or inclined a little up or down (positions 315°-0°-55° of Fig. 7), then the nystagmus during the rotation round the vertical axis is purely horizontal, but if the head is placed in another position, the nystagmus represents a complicated movement, which cannot be simply described. This is an important statement, as it shows us again that the labyrinth brings forth normal reactions only when it is stimulated under physiological conditions, *i. e.*, when the rotations of the head are similar to those of which the free animal makes use.

As we wish here to study chiefly only those muscle contractions which bring about the physiological eye movements, we shall refer in Chapter VI exclusively to centric rotations with the head in a physiological position.

II. The Nystagmus of the Eye Muscles Produced by Stimulation of One Semicircular Canal.

We shall not take up now the question in which plane the eye nystagmus set up by stimulation of one semicircular canal occurs. This is today still an entirely open question, as the frequently repeated assertion that each semicircular canal brings about a nystagmus in its own plane, is not quite correct. I have already often

enough pointed this out, and should like to emphasize that sometimes currents of opposite directions in one semicircular canal give rise to nystagmuses in different planes. In the case of head movements a semicircular canal may produce reactions in its plane (compare Ewald[18] and Breuer[14, 15] in pigeons, Rothfeld[60] in rabbits); the same may be true for the reactions of the body and limbs (see Mach[51] and Bárány[7] in rabbits, Tait and MacNally[62] in the frog,

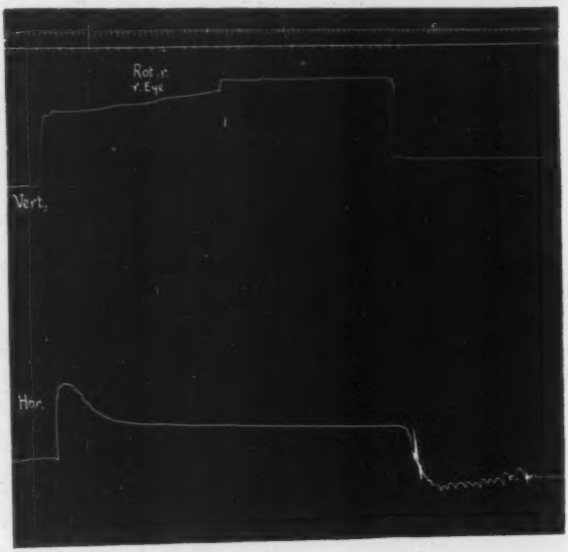


Fig. 43. Tracings of the horizontal and vertical components of the eye reflexes in the case of a rotation to the right. Head in the normal position; rabbit in position 4 of Fig. 26. The distance of the head from the axis was 40 c.m.
The upper tracing (vert.) shows the vertical component of the movement; lifting of the tracing indicates a vertical movement downwards.
The lower tracing shows the horizontal component of the eye movement; lifting of the tracing represents a horizontal movement backwards.
The components of the eye movement are analyzed by means of two silk threads attached to the center of the cornea and reflected in pulleys.
The rotary component does not appear in the tracings.

Maxwell[54] in fishes), but in the case of the eye, especially when it is a case of stimulation of the vertical semicircular canals, it happens often that the eye movements occur in a different plane. I have often observed this during caloric stimulation of the semicircular canals and when artificial currents were brought about through a fistula in the bony canals. My coworker, P. de Juan[35], found proof

of my statements. There still is much work to be done in this direction.

As already mentioned above theoretical attempts have been made in the literature to determine which muscles bring forth a certain nystagmus and which muscles are dependent upon each semicircular canal. No theoretical treatment is able to give the solution of this problem.

The tables on Fig. 44 represent the nystagmus set up in the single muscles by stimulation of the semicircular canals. The data on

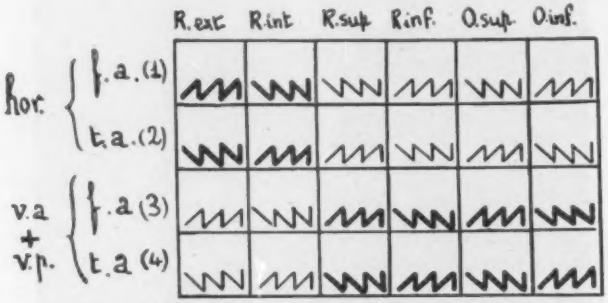


Fig. 44. The nystagmus of the eye muscles set up by stimulation of the semicircular canals. (hor. c.) horizontal canal; (vert. ant. c.) vertical anterior canal; (vert. post. c.) vertical posterior canal; (f. a.) lymph current from the ampulla; (t. a.) lymph current towards the ampulla.

The signs in the table correspond to the tracings written by the muscles on the kymograph, i. e., lifting of the line represents contraction; lowering, relaxation; the vertical lines represent the quick phase.

The signs in heavy lines represent the nystagmus, the direction of which, with the exception of very special cases, cannot be reversed through another concurrent stimulation; the signs in thin lines, the nystagmus, which can be easily reversed if the excitation of the semicircular canal happens to coincide with other stimulations.

The lymph currents (1 and 3 or 2 and 4) are set up simultaneously if the rotation of the vertical axis takes place with the head in one of the positions 0°-90° of Fig. 7.

The lymph currents (1 and 4 or 2 and 3) are set up simultaneously if the rotation on the vertical axis takes place with the head in one of the positions 0°-270° of Fig. 7.

This table corresponds to the muscles of the right (left) eye in the case of excitations of the right (left) labyrinth. In the case of excitations of the right (left) labyrinth and the muscles of the left (right) eye, the direction of the nystagmus is the opposite.

the ground of which the tables were composed have been obtained from three kinds of experiments.

a. Rotations of the animal round the vertical or horizontal axis with the head in such a position that either only the external or only the two vertical canals could be stimulated.

b. Rotations of the animal round the vertical or horizontal axis after both external or the four vertical canals were plugged after the method of Ewald.

c. Caloric stimulation of the individual canals.

These experiments give consistent results when the animal is turned with its head in a physiological position; when the position of the head is not physiological, there may be obtained very complicated results, a good example of which is given in Figs. 42 and 45.

At present we may state that each semicircular canal may produce nystagmus in both directions in all muscles and in fact produces it in many cases. The results seem to depend in a high degree on

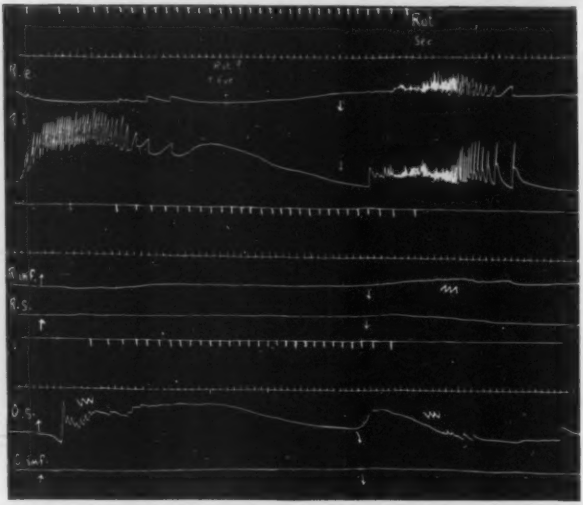


Fig. 45. Reactions of the six eye muscles to a rotation to the right. Head in position 215° of Fig. 7. Rabbit in position 1 of Fig. 26 (the rotation axis passes between both labyrinths); therefore there are no reflexes due to the centrifugal force. The rotation is started and stopped slowly, the third reaction is therefore absent.

To note that the o. sup. shows the same nystagmus at the beginning and at the end of the rotation; the horizontal and vertical muscles show the nystagmus that corresponds to the tables in Fig. 44.

the position of the head in space. The tables on Fig. 44 can certainly be regarded, under such conditions, only as provisional; they are, however, of great value, as they open a new problem, namely that the excitations coming from the single semicircular canals are almost in every case in some way antagonistic and consequently demand that the central nervous system harmonize them; I hope to be able to publish very soon an extensive paper on this problem.

III. The Third Reaction to Rotations.

Rotation innervation does not always bring forth nystagmus in every muscle; in many cases it is possible to find in the muscles another reaction, which I have named "the third reaction to the rotation"[45]. A separation between nystagmus and the third rotation reaction is justified by different conditions, but, on the other hand, it represents a schematization of the question, because the third rotation reaction is produced most strongly in those muscles which show either a very weak nystagmus or none at all and in this case the eye nystagmus is brought about by the nystagmus of some mus-

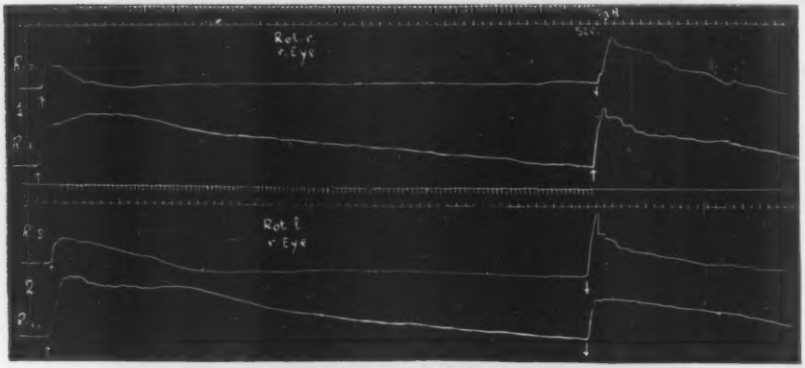


Fig. 46. Reactions of the vertical muscles to rotations. 1. Rotation to the right; 2. rotation to the left. Head in the normal position; rabbit in position 1 of Fig. 26. (The rotation axis passes between both labyrinths.) There are no reflexes due to the centrifugal force.

These tracings demonstrate the third reaction in the case of centric rotations. Both muscles contract at the beginning of the rotation as well as at the end; the contractions pass slowly away.

These tracings are obtained with the same rabbit as in Figs. 29-34. The comparison of Fig. 45 and Fig. 29 shows the differences in the third reaction in the case of centric and eccentric rotations; if the rotation is centric the third reaction at the beginning and at the end of the rotation are alike.

cles and by the third rotation reaction of the other muscles. In this publication I must refrain from detailed treatment of this question, as I have recently given a systematic account of the main results[50]. Fig. 46 contains examples of the third rotation reaction during centric, and Figs. 29-34 of the third rotation reaction during eccentric rotations.

There must exist a certain relation between nystagmus and the third reaction. Through strong caloric stimulation of the horizontal semicircular canals a reflex reaction, similar to the third rotation

reaction, may be set up in the vertical muscles when the head is held in the neighborhood of the normal position in space; but if the head is held in the lateral position the vertical muscles show always nystagmus[40].

IV. The Interaction of the Semicircular Canals.

In most cases of rotations all the three pairs of semicircular canals will be excited at the same time, as the rotations take place generally in such a way that none of the canals lie in the rotation plane. We shall not take up now the physical side of the question, which has been studied by Favill[19] and by me[48, 49]. Favill made use of a glass model of the labyrinth, and I carried out mathematical calculations of the streams induced in one canal lying vertically to the rotation plane by the stream in another canal lying in the rotation plane. The whole body of evidence seems to be sufficient to justify the conclusion that the currents of lymph in the single canals do not influence each other and, therefore, the semicircular canals work as if they were anatomically independent from each other.

The biological side of the question, as can be seen from the tables of Fig. 44, is especially complicated. These tables show that in the case of the rotation of the head round the vertical axis with the head in one of the positions of Fig. 7, the currents in the individual canals would produce nystagmus of different direction in certain eye muscles, if they were brought about successively instead of being set up simultaneously.

The currents in both horizontal semicircular canals set up by rotations of the head will always produce the same results, because a current from the ampulla on the right side brings forth the same reflexes as a current towards the ampulla on the left side, and conversely.* The same may be said of the vertical semicircular canals, because currents towards the ampulla in one labyrinth are combined with currents from the ampulla in the other labyrinth.

But the currents in the horizontal canals, on one hand, and those in the vertical canals, on the other hand, are always partly antagonistic, because when they are antagonistic with reference to the nystagmus of the horizontal muscles, they are antagonistic with reference to the nystagmus of the vertical muscles, and conversely.

During the rotations of the head round the lengths axis currents appear only in the vertical canals, and they are always antagonistic,

*Recently M. H. Fischer[21] has described in humans a series of reflexes produced by simultaneous stimulations of both ears with cold or warm water. In these cases the currents in the horizontal canals are of the same direction in both labyrinths. I hope to be able to publish soon a series of experiments bearing on this question. Explanations for the nystagmus have been offered by Barany and Quix.

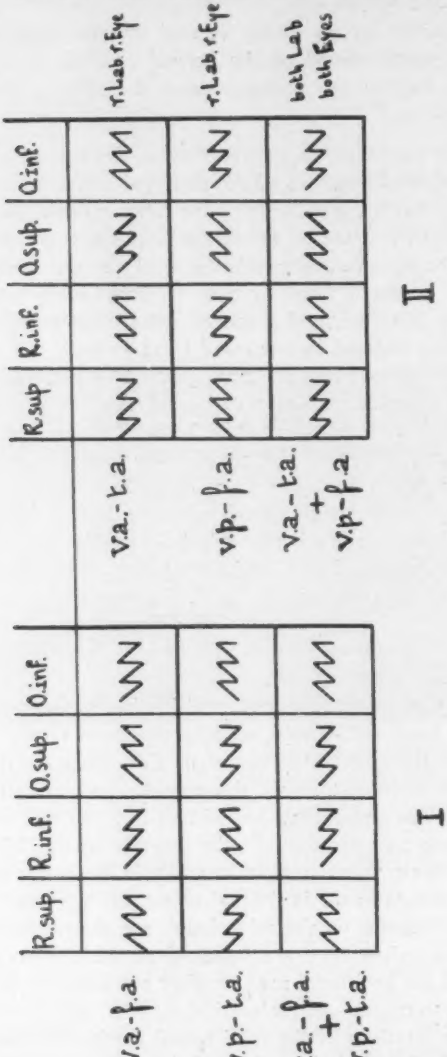
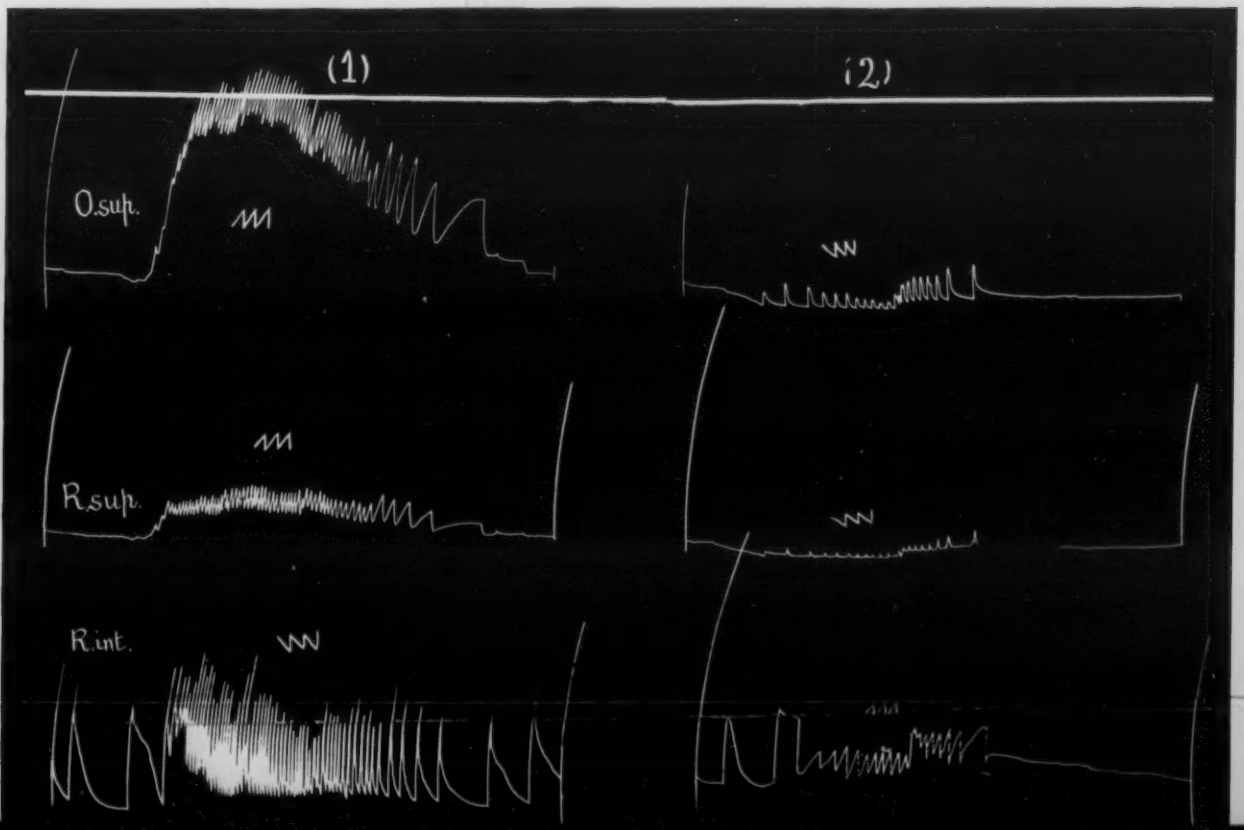


Fig. 47. Nystagmus set up in the vertical and oblique muscles when lymph currents are induced in the vertical semicircular canals; I (v. a.-f. a.) current from the ampulla in the vertical anterior canal; (v. p.-t. a.) current towards the ampulla in the vertical posterior canal; (v. a.-f. a. + v. p.-t. a.) current from the ampulla in the vertical anterior canal plus current towards the ampulla in the vertical posterior canal. II (v. a.-t. a.) current towards the ampulla in the vertical anterior canal; (v. p.-f. a.) current from the ampulla in the vertical posterior canal; (v. a.-t. a. + v. p.-f. a.) current towards the ampulla in the vertical anterior canal plus current from the ampulla in the vertical posterior canal.

The direction of the nystamus of the horizontal muscles, although it is always of great amplitude (Fig. 48), is not indicated in the tables, because the direction of this nystagmus may change under various circumstances, as I shall describe it in another paper.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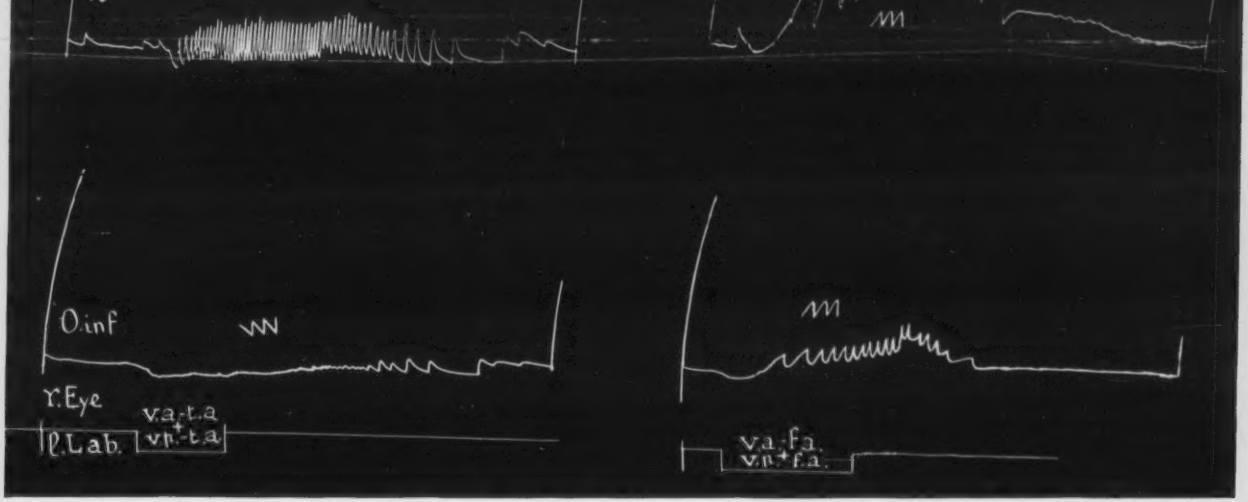


Fig. 48. Nystagmus set up in the muscles of the right eye by excitations of the vertical canals of the left labyrinth.

The six eye muscles write their reflexes simultaneously; the kymograph is equipped with six writing levers and each of them is connected with one of the six eye muscles.

The semicircular canals have been liberated in one point by taking away the surrounding bone. Cold or warm needles have been applied simultaneously to the vertical canals in order to produce currents towards the ampulla or currents from the ampulla in both canals. The signal at the bottom gives the duration of the contact of the needle with the bony canal. The speed of the kymograph is the same as in Fig. 49.

Head in the normal position. 1. Currents towards the ampulla in both canals; 2. current from the ampulla in both canals.

The six muscles show nystagmus in both cases; the direction of the nystagmus corresponds to the data contained in the tables of Fig. 44.

because the currents towards the ampulla in one labyrinth and currents from the ampulla in the other labyrinth will produce the same reflexes.

During the rotation of the head round the bitemporal axis the conditions are quite different. Currents towards the ampulla in the two anterior vertical canals are accompanied by currents from the ampulla in the two posterior vertical canals, and conversely. The tables on Fig. 47 show, first, that the lymph currents, either towards the ampulla or from it, set up simultaneously in both labyrinths, are antagonistic and, second, that currents towards the ampulla in the anterior vertical canals and currents from the ampulla in the posterior vertical canals, or conversely, are also partly antagonistic.

The summation of the stimuli coming from the single canals is not an algebraic one.

The reader may find in my former publications[48, 49] the experimental treatment of this question.

I should like to stress the point that the nystagmus of the horizontal muscles, as a rule, has the strongest amplitude, even in the case of stimulation of the vertical canals (see Fig. 48); and that the nystagmus set up by excitation of the horizontal canal has a stronger frequency than the nystagmus produced by excitation of the vertical canals (see Fig. 49).

No simple laws can be applied to combinations of antagonistic currents in the vertical canals, *i. e.*, if currents towards the ampulla in the anterior vertical canals and currents from the ampulla in the posterior vertical canals, as there are not enough experiments yet available. The following three kinds of experiments: *a.* rotations round the bitemporal axis with the head in the normal position in space taken as the starting (initial)position of the rotation; *b.* rotations round the vertical axis with the head in the lateral position with the studied eye above; and *c.* caloric excitation of the canals, have given the results summarized in the table of Fig. 47. Table I gives the following:

1. The kind of nystagmus of the individual eye muscles as a result of a current from the ampulla in the anterior vertical canals in the labyrinth on the same side (in the muscles of the other eye the nystagmus has the opposite direction).

2. The same—as a result of a current towards the ampulla in the posterior vertical canal on the same side (in the other eye the nystagmus has the opposite direction).

3. The same—in the case of a combination of the above mentioned currents. The nystagmus has the same direction in the muscles of both eyes.

This combination of currents takes place at the beginning of the rotation of the head downwards round the bitemporal axis, the eye motion (see Chapter I) consists then of a rolling of the eye with the upper pol of the cornea backwards.

In Table II is given:

1. The nystagmus of the individual muscles as a result of a current towards the ampulla in the vertical anterior canal of the labyrinth on the same side (in the muscles of the other eye the nystagmus has the opposite direction).

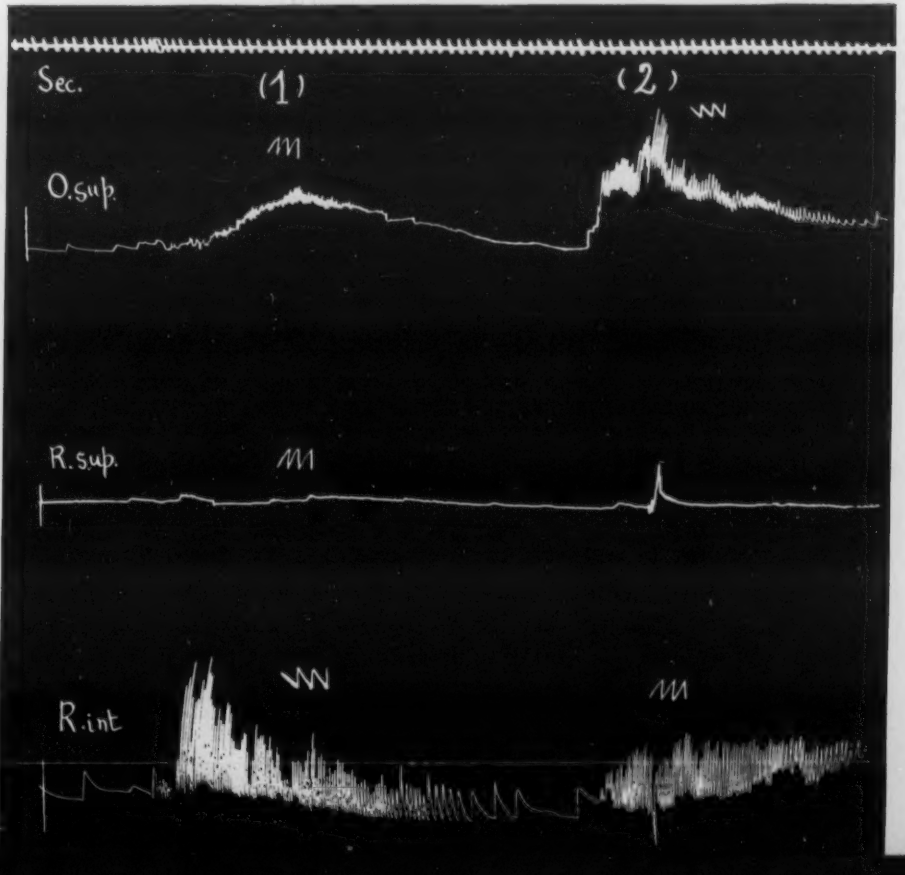
2. The same—as a result of a current from the ampulla in the posterior vertical canal on the same side (in the other eye the nystagmus is in the opposite direction).

3. The same—for the combination of both currents. The nystagmus has the same direction in both eyes.

This combination of currents takes place at the beginning of the rotation of the head upwards round the bitemporal axis; the eye motion (see Chapter I) consists of a rolling of the eyes forwards.

It is interesting to mention that the data reproduced in this table do not correspond with the known rule of Ewald. Ewald found that the currents from the ampulla in the vertical canals have twice as strong an effect as the currents to the ampulla. Therefore it has to be expected that the current from the ampulla should always determine the direction of the nystagmus. In opposition to this, we find, however, that the stimulus from the anterior vertical canal, independent of the fact whether it is brought about by currents to the ampulla or from it, always determines the direction of the nystagmus of the vertical muscles of the eye on the same side and of the oblique muscles of the eye on the other side; whereas the current of the posterior vertical canal always determines the direction of the nystagmus of the oblique muscles on the same side and the vertical muscles on the other side.

In former publications[47, Chapter XI; 50, p. 105] I have also shown other important facts which speak for themselves against the validity of Ewald's rule; I wish to bring this to the reader's attention. There is no doubt that there must be something correct in Ewald's rule, because during experimental stimulation of the semicircular canals reactions often appear which seem to be dependent on this law; but the experimental facts which speak against the validity of this rule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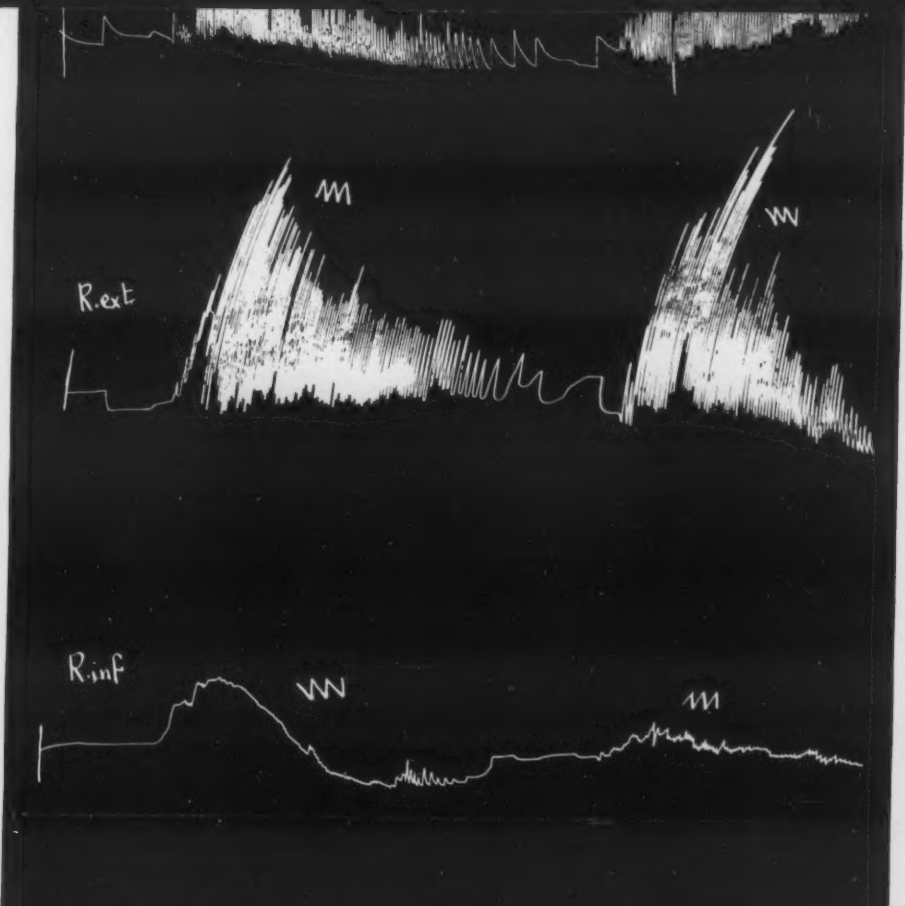
R.ext
R.inf

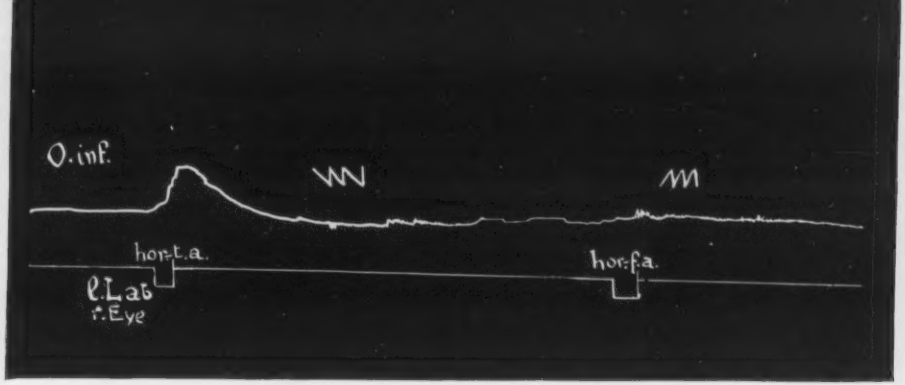

Fig. 49. Nystagmus set up in the muscles of the right eye by excitation of the left horizontal canal.

The six muscles write their reflexes simultaneously. The currents in the canal are produced by applying a cold or warm needle to a point of the canal, which has been liberated from the surrounding bone. Head in position 50° of Fig. 7. 1. Current towards the ampulla; 2. current from the ampulla.

The upper signal at the bottom gives the duration of the contact of the needle with the canal.

All the six muscles show nystagmus; r. ext. and r. int. in the direction indicated in Fig. 44; the other four muscles in the opposite direction to that indicated in Fig. 44. (Another paper dealing with this phenomena will soon appear.)

To note that the nystagmus set up by excitation of the horizontal canal is much stronger than the nystagmus following excitation of the vertical canals (Fig. 48).

To note that o. sup. and r. inf. during the nystagmus show an increase in tonus, which does not correspond to the slow phase of the nystagmus.

are quite as numerous and, to be sure, of greater importance. We may not forget that Ewald's rule was stated more than forty years ago, at a time when the knowledge of the labyrinth function was still but very small and the function of the nervous system could not be considered at all. Besides there are still some facts in Ewald's experiments, as, for instance, the appearance of only the slow phase of the nystagmus in the case of undoubtedly maximal stimulations of the canals, that we can by no means explain[47, Chapter XI, §5]. To repeat Ewald's experiments is one of the most important tasks we have to accomplish in order to throw some light on the mechanism of excitation of the semicircular canals.

V. The Dependence of the Reflexes Set Up by Stimulation of the Semicircular Canals on the Position of the Head.

Bárány[4, 5] was the first to notice that one and the same stimulation of a canal may produce somewhat different results, when the position of the head in which the stimulation of the semicircular canals takes place is different.

In issuing this statement Bárány has based himself on the following observations: When a rabbit is being turned with its head pointing vertically downwards or upwards round a vertical axis, according to the theory of Breuer, the same kinds of currents develop in the semicircular canals; the nystagmus, according to Bárány, should be in each case brought forth by different muscles; consequently it is necessary to assume that the excitation of the canals undergoes a change in the nervous system as a result of the position innervation, which takes place simultaneously. Rothfeld[60] and Hoshino[32] have accepted the theory of Bárány. The body of evidence offered by Bárány with reference to the eye reflexes may seem today perhaps not quite conclusive* because all the six eye muscles show nystagmus in both head positions, but I have conducted experiments[49, 50] which seem to put Bárány's theory beyond criticism; some samples will be mentioned here.

In Fig. 50 are reproduced reactions of the horizontal muscles of the right eye to rotations of the head round the lengths axis. In 1, are shown four rotations of 90° to the left, and in 2, four rota-

*Barany has, however, pointed out that the past pointing reaction of the arm takes place always in the same direction quite independently of the position of the arm. This observation seems to prove the influence of the postural innervation on the motion reflexes quite conclusively. It is of interest to quote this obseravtion of Barany as it represents one of the first cases of "reflex reversal" which has been described and, to be sure, the first well established case of "postural" reversal. The significance of the postural reversal of the reflexes for the theory of the labyrinth function cannot be too strongly emphasized.

tions also of 90° to the right. In the beginning of the rotation, the head was placed in different positions in space. The rotation reaction of the r. ext. should have consisted of a relaxation at the beginning of the rotation to the right, and of a contraction at the beginning of the rotation to the left. The reaction of the r. int. should have been always the opposite one. The tracings, however,

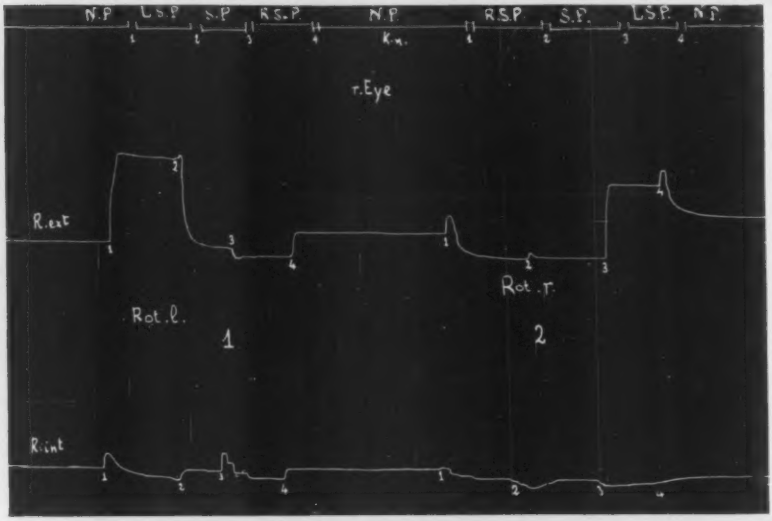

Fig. 50. Reactions of the horizontal muscles of the right eye to rotations of the head on the lengths axis of the body (longitudinal rotation, Fig. 13).
1. Four rotations to the left; 2. four rotations to the right. Each rotation (1, 2, 3, 4 on the signal at the top and on the tracings) of 90°, was started quickly and continued with diminishing speed until the turn table came to rest, in order to avoid the postrotary reaction. After each rotation the turn table remained still during several seconds; the head assumed in each case a different position in space noted on the signal line at the top of the figure. There is no time signal but the drum rotated approximately with the same speed as in the other figures.
To note that the reaction of the muscles at the beginning of the rotation is not always the same, depending on the position of the head at the start of the rotation; and further that both muscles sometimes show simultaneous contractions.
(N. P.) normal position; (L. S. P.) left side position; (S. P.) supine position; (R. S. P.) right side position.

show that the reaction of the muscles were different in each position of the head. But when the animal was turned several times to the right or to the left, there was always present, at the end of the rotation, a nystagmus in the direction, which had to be expected from the table on Fig. 44.

Similar phenomenons are found in Fig. 51, which show rotation reactions and position reflexes of the oblique muscles under similar

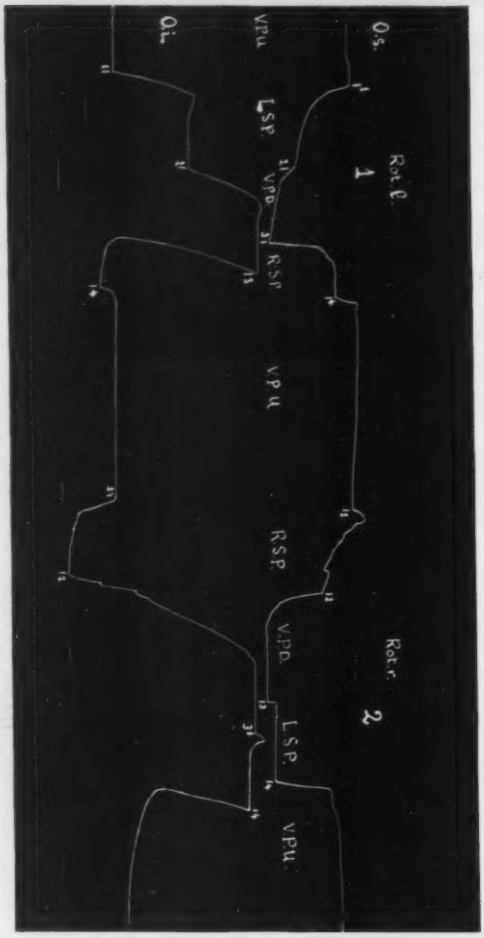

Fig. 51. Reactions of the oblique muscles of the right eye to rotations on a horizontal axis; head at the beginning of the rotation in the position head vertical, muzzle upwards (dorsoventral rotation, as in Fig. 21).

1. Four rotations of 90° to the left; 2. four rotations of 90° to the right. The rotations were administered as in Fig. 50. Between each two rotations a pause of several seconds.

To note that the reactions at the beginning of the rotation are not always the same, and that the rotation reactions correspond almost exactly to the tonic reflex due to the change of the position of the head (Chapter VII).

(V. P. U.) vertical position, muzzle upwards; (L. S. P.) left side position; (V. P. D.) vertical position, muzzle downwards; (R. S. P.) right side position.

conditions. The size of the rotation reaction was, in every case, different, and its direction was not always the same.

If continuous rotations are being administered, at the end of the rotation, a nystagmus will always be found, which, in most rabbits, has the direction which had to be expected from the table on Fig. 44; in some rabbits, however, the nystagmus has different directions in different positions of the head (see Fig. 42). The direction of the nystagmus is then as much dependent on the position of the head, as on the direction of the lymph currents.

VI. Conditions Under Which Nystagmus Is Brought Forth in the Individual Eye Muscles.

It has been already mentioned that one canal may set up a nystagmus in all eye muscles and that the position of the head may influence this nystagmus. It seems, however, that there is no simple rule, which could ascertain in which position of the head a muscle should show nystagmus. The only rule that we can state is perhaps the following: When a muscle, as a result of position innervation, finds itself in a state of relaxation, it will show either no nystagmus or only a very weak one. This rule, however, has many exceptions and its value consists in the fact, that it may help us to arrange our experiments; when we wish to study the nystagmus in a certain muscle, we must bring the head in such a position in which this muscle has a high tonus.

CHAPTER VI.

Laws Controlling the Activity of Eye Muscles During Eye Movements.

The activity of the eye muscles in the case of nystagmus is controlled by the law of reciprocal innervation. The eye muscles may be divided into three pairs of antagonists (r. ext. + r. int.; r. sup. + r. inf.; o. sup. + o. inf.) and both muscles of each pair are innervated reciprocally.

The law of reciprocal innervation reads usually as follows: "If one muscle contracts its antagonist relaxes." Expressed in this way this law shows numerous exceptions in the case of eye movements. It is possible, however, to somewhat modify it and make it generally applicable to the nystagmus: "Two muscles of the same pair never show nystagmus in the same direction," *i. e.*, when one muscle shows a nystagmus with a quick contraction phase its antagonist shows nystagmus with a quick relaxation phase, or remains quiet." This definition of the law of reciprocal innervation is necessary because it is often the case that one muscle remains in a state of unchanged tonus, while its antagonist shows nystagmus, and because it is possible to observe often that the muscles during nystagmus show changes in tonus, which may be the same in antagonistic muscles. Therefore, it is necessary, too, to emphasize that this law is only applicable to the nystagmus. Under nystagmus we understand only the rhythmic reflex, which consists of repeated slow contractions (relaxations), followed by quick relaxations (contractions).

That the muscles during nystagmus may show postural tonus changes was already observed by Bartels[10]; they appear in the graphic records as a lifting or lowering of the whole tracing. Bartels has even observed a lowering of the tonus in the same direction in both horizontal recti.

Bartels found that the tonus change of the muscles takes place in the direction of the slow phase of the nystagmus and he saw in this the expression of the known deviation of the eyes.

When the rotation is centric, *i. e.*, when the rotation axis passes between both ears, the tonus changes in the horizontal muscles occur in the direction of the slow phase of nystagmus. But in case of eccentric rotations or in the vertical and oblique muscles during both centric or eccentric rotations the direction of the slow phase of nystagmus and that of the change of tonus may be different, and, there-

fore, antagonistic muscles may exhibit the same tonus changes. We find examples of this in Figs. 28 and 52. In the case of eccentric rotations the eye deviation which accompanies the nystagmus is quite different from that which appears in the case of centric rotations. The tonus changes of the vertical and oblique muscles at centric rotations do not cause any eye deviation (see later).

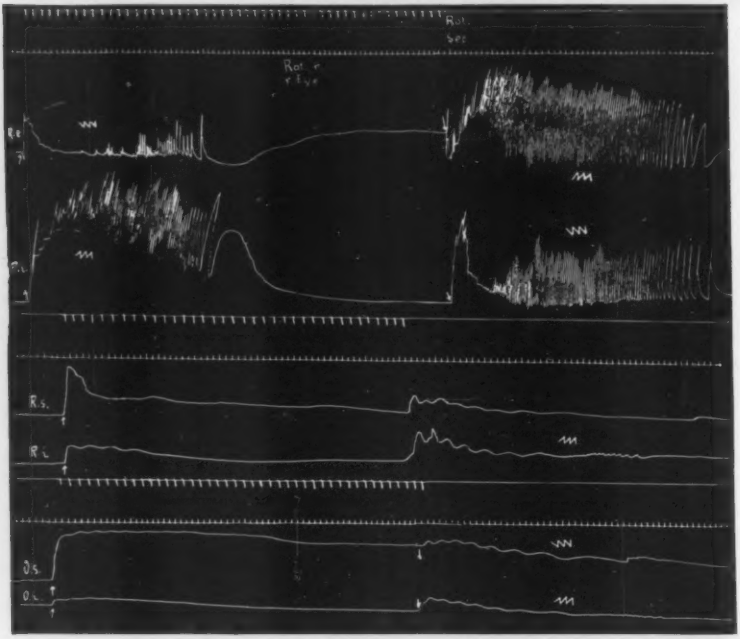

Fig. 52. Muscle reflexes which bring forth the horizontal eye nystagmus. Muscles of the right eye. Rotations to the right. Head in the normal position; rabbit in position 1 of Fig. 26, i. e., the rotation axis passes between both ears. The rotation starts and stops quickly.

The horizontal muscles show a strong nystagmus and the vertical and oblique muscles tonus changes of the same direction in all four, and a very small nystagmus.

There are two groups of synergists, R. ext. + r. inf. + o. inf., and r. int. + r. sup. + o. sup.

Each contraction or relaxation of the horizontal muscles represents a horizontal eye motion; the vertical and oblique muscles do not change their tonus during the nystagmus, i. e., during the horizontal eye movements.

The eye nystagmus, and, to repeat once more, we understand under nystagmus only rhythmic movements, is exceptionally set up only by two muscles and, usually, by all six muscles.

An eye nystagmus brought forth only by two muscles is to be found in rabbits only in one case and only in some rabbits, namely

when the animal, with its head in the normal position in space, is being turned round the vertical axis (see Fig. 52). The pure horizontal nystagmus is being brought forth by both horizontal muscles. The other four muscles do not remain quiet, but show an increase in tonus.

The co-operation of the vertical and oblique muscles is absolutely necessary in order that the horizontal muscles may produce a pure horizontal eye movement. As mentioned above (see Chapter II) when the vertical and oblique muscles are made inactive the horizontal

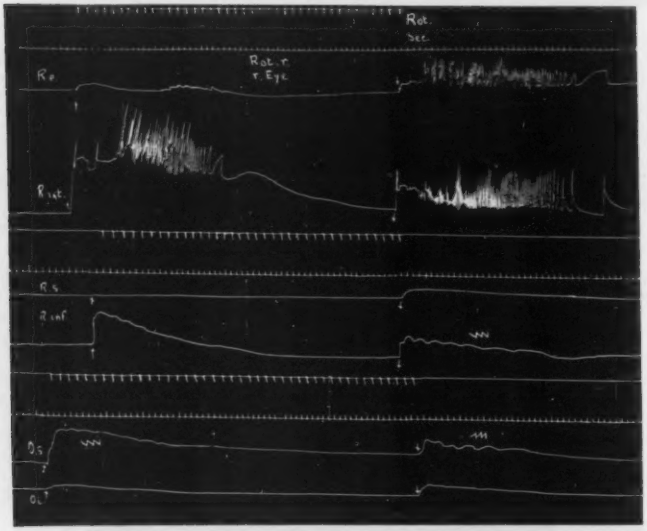

Fig. 53. The same as in Fig. 52 when the head finds itself bent 55° upwards (Fig. 7 shows the position of the eye in the orbit).
The changes in tonus of the vertical and oblique muscles are not the same as in Fig. 52; on the other hand, the nystagmus of the vertical and oblique muscles has reversed its direction and now the groups of synergists are: r. ext. + r. sup. + o. sup. and r. int. + r. inf. + o. inf.

muscles bring forth a diagonal eye movement forwards and upwards or backwards and downwards, accompanied by a slight rolling. The simultaneous contraction of the vertical and oblique muscles corrects the action of the horizontal muscles; these contractions are also necessary in order to hold the eye rotation center in an unchanged position.

If the head finds itself in any other position than those which we have formerly named "physiological positions" (see Fig. 7—315°-0°-55°), the nystagmus, in the case of the rotation round a vertical

axis, is also horizontal, but as the eye is no more in the primary position the simple tonus changes of the vertical and oblique muscles are not sufficient to correct the secondary actions of the horizontal muscles. Therefore, always several and often all six muscles show a nystagmus; the strongest, however, being that of the horizontal muscles (see Figs. 53 and 54).

The tables on Fig. 44 show in which manner the nystagmuses of the individual muscles are combined. If the head during the rotation lies inclined upwards, there takes place in the semicircular canals a combination of currents which causes the following muscle

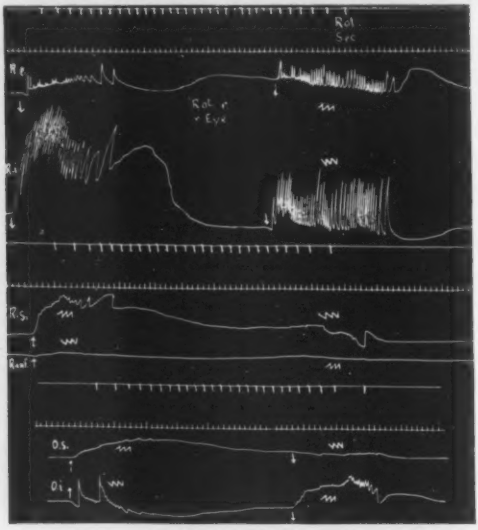

Fig. 54. The same as in Fig. 52 when the head finds itself bent 55° downwards (Fig. 7 shows the position of the eye in the orbit which corresponds to this position of the head in space). All the six muscles show nystagmus; the groups of synergists are: r. ext. + r. inf. + o. inf. and r. int. + r. sup. + o. sup. The changes in the tonus are, with the exception of the r. inf., in the direction of the slow phase of the nystagmus.

associations: r. ext. + r. sup. + o. sup. are synergists and show nystagmus in the same direction; r. int. + r. inf. + o. inf. are also synergists and show nystagmus in the same direction; both groups act as antagonists of each other (see Fig. 53).

If the head lies inclined downwards, the groups of synergists are, on one hand: r. ext. + r. inf. + o. inf., and, on the other hand: r. int. + r. sup. + o. sup. Both groups act as antagonists of each other (see Fig. 54).

The horizontal movement of the eye is always being brought forth by one of these two kinds of muscle combinations, but for each eye position the combination is somewhat different, because the amplitude of the nystagmus of each individual muscle is every time different.

If the eye is rolled forwards, because the head lies inclined upwards, the vertical and oblique muscles, as long as the eye exercises pure horizontal movements, show only a weak nystagmus (see Fig. 53). The nystagmus of these muscles is, however, of a large amplitude (see Fig. 54) when the eye is rolled backwards (head inclined downwards of the horizontal plane).

If the head position is no more a physiological one, that is if the inclination of the head measures more than 50°-60°, then the vertical and oblique muscles show nystagmus of as large an amplitude as the horizontal muscles, but the eye movements are then not horizontal, but very complicated.

The change in tonus of the muscles are also each time somewhat different; nevertheless, it is impossible to issue a rule of general validity. The only rule which could be stated is the following: When the nystagmus of one muscle is of small amplitude, the tonus change during the nystagmus may occur in the opposite direction of the slow phase of the nystagmus. When the nystagmus, however, is of greater amplitude, the tonus changes and the slow phase of the nystagmus usually have the same direction. It can be further stated that, usually muscles, which are in a state of tonic relaxation, show a nystagmus of smaller amplitude than the muscles, which exhibit a higher tonus, but the postural change of tonus may be just as large or even larger.

At present it is still impossible to explain how the muscle contractions hold the eye rotation center fixed in the orbit, when the eye, starting from a secondary position, moves horizontally. The explanation is comparatively easier when the starting position of the eye is the primary one. The vertical and oblique muscles do nothing else as increase their forces, consequently, no changes occur in the mechanism, which holds the rotation center fixed in the orbit during the state of rest of the eye, *i. e.*, the resultant of the forces of the four vertical and oblique muscles remains unchanged during the whole horizontal excursion. This can be explained by the fact (see Chapter III) that the action of one muscle does not change when it moves the eye in its own direction and, therefore, the action of the horizontal muscles always requires the same correction during the whole horizontal excursion of the eye.

If the eye starts from a secondary position, the conditions are more complicated, because the insertions of the horizontal muscles have a different position in the orbit and, therefore, the forces developed by them, if working alone, would bring about very complicated eye motions. This may explain why the vertical and oblique muscles, instead of an increase of tonus accompanied by a small nystagmus, must show a stronger nystagmus with various postural changes; however, it seems not to be possible to explain in detail the action of the individual muscles.

Summarizing the above mentioned we may say: The horizontal movements of the eye are being brought about by different combinations of muscle contractions and relaxations; there is a certain combination of muscle activity for each initial position of the eye. All these combinations, however, may be divided into two groups, of which one is used when the horizontal eye movement takes place on the ground of a rolling of the eye forwards, and the other one when the horizontal movement is superimposed to a rolling of the eye backwards. Some muscles show nystagmus, for which the law of reciprocal innervation is followed and they also may show, in addition to nystagmus, tonus changes, for which the law of reciprocal innervation cannot be applied, evidently because these tonus changes serve for the purpose of holding the rotation center and rotation axis of the eye in a fixed position. The change of tonus in the vertical and oblique muscles, which may be very considerable, does not bring about a change in the position of the eye and, therefore, can only be demonstrated by actual recording of the reflexes.

Further research in this line is now under way.

CHAPTER VII.

The Combination of Postural and Motion Reflexes.

In Chapters II and III the position reflexes were studied and in Chapter V the motion reflexes; we must, however, study, too, the combination of these two kinds of reflexes, as in the free animal only very seldom pure position or motion reflexes take place. Pure postural reflexes may be observed only when the animal rests with its head in the normal position in space; each other head position is maintained only for a very short time. On the other hand, motions of the head are very often accompanied by changes in position.

Hoegyes accepted that in the case of a rotation of the head round the horizontal axis the motion of the eye as a result of the rotation reflex, and the change in the eye position due to the new position of the head—are identical; the only difference consists in the appearance of a nystagmus at the end of the movement, when the speed of the rotation is high.

Magnus and de Kleyn[52] have reached a similar point of view.

The problem is, however, more complicated; we shall now take up some of the questions, yet with the understanding that the answers may only be sketched. In order to simplify the matter, we shall restrict ourselves to the study only of the head rotations used by the free animal, *i. e.*, rotations round the bitemporal or lengths axes between points 300°-0°-60° (see Figs. 7 and 13).

If one takes the rabbit in the hands and rotates its head passively one finds that the motion and position reflexes are seldom identical, already because the excursion of the eye is generally larger than the position reflex. It is, however, impossible to obtain exact data through direct observation.

The study of the reflexes on the eye muscles themselves is more instructive, as they give us precise data. If the rotation of the head is administered with constant speed, and suddenly stopped, there takes place at the end of the rotation an after reaction (post-rotary nystagmus) in the opposite direction of the position reflex, or, if the speed of rotation is less, the muscles show at the end of the rotation too strong contractions or relaxations, which gradually decrease until the muscles reach the state of tonus which correspond to the new head position. This represents a slow backwards directed eye movement.

There is, however, a certain kind of rotation which does not bring forth any after reaction; at the end of such a rotation the muscles reach the state of tonus in which they then will remain (see Fig. 51); this rotation must represent the physiological kind of rotation, *i. e.*, the rotation used by the free animal; it is quickly started and continued with a decreasing speed until the movement ceases. In another publication[46] I have handled this question in detail and explained that the speed of the rotation of the head is also automatically regulated by the labyrinth. The labyrinthine innervation taking place at

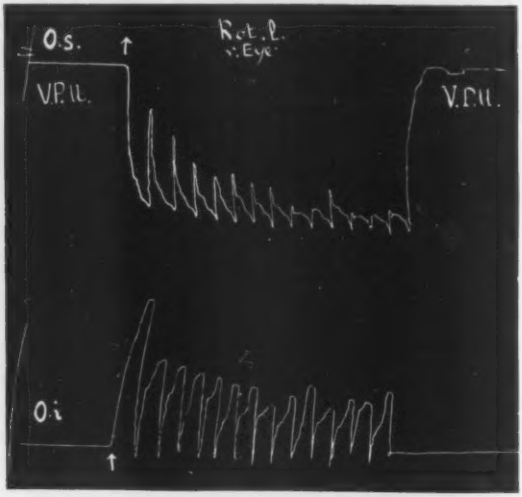

Fig. 55. Reactions of the oblique muscles to rotations of the head on the horizontal axis (dorsoventral rotation). The rotations (13) takes place under the same conditions as in Fig. 21, the only difference is that here the speed of the rotations is many times greater. In Fig. 21 the tracings were not reciprocal, but here the innervation of the muscles is true reciprocity. (Change of position innervation into motion innervation.)

the beginning of the rotation brings about a reflex, which aims to turn the head in the opposite direction, *i. e.*, to arrest the undergoing rotation of the head. The intensity of this reflex depends, of course, on the speed of the head rotation, so that the quicker the rotation is started, the quicker is it slowed down. During the movement of the head a number of reflexes (on the eye, on the neck, on the limbs, etc.) are brought forth; but these reflexes disappear at the end of the rotation, without leaving any disadvantageous post-rotary reaction.

Through this simple mechanism the amplitude of the eye movement produced by the motion reflexes is adapted to the position reflex brought forth by the change in the position of the head; there are, however, other kinds of adaptations, of which the following examples give a good idea.

The muscle reflexes caused by a quick and slow rotation of the head (pure change in position) are not always qualitatively equal.

When the head is turned to the left round the lengths axis an excitation of the semicircular canals takes place, which is supposed to cause a relaxation of the r. ext. (see Fig. 44); the corresponding change in the head position, however, brings forth a contraction of the r. ext. (see Fig. 23). Both kinds of reflexes are, thus, antagonistic. In Fig. 50 we find that the r. ext. (see Fig. 50, I, 1) has shown a contraction, *i. e.*, the motion reflex has undergone a considerable modification, in view of the position reflex.

If the head is rotated upwards round the bitemporal axis, the motion reflex in the oblique muscles should always consist in the contraction of the o. sup. and a relaxation of the o. inf. between points 270° and 0°, but between positions 0° and 90° the o. inf. remains usually in a state of unchanged tonus; on the other hand, the contraction of the o. sup. must be of different strength in each section of the motion, thus, every time the motion reflex must be modified in order to adapt it to the position reflex.

As to the laws regulating the association of the eye muscles, we find the same conditions in the case of quick rotations of the head round the horizontal axis, as in the case of rotations round the vertical axis. The muscles which bring forth the eye movements are innervated reciprocally (see Chapter V), but muscles which serve mainly for the purpose of holding the rotation center of the eye fixed in the orbit and of correcting the secondary actions of the main muscles, are not always innervated reciprocally. A good example of this give the curves on Fig. 50, where the horizontal muscles sometimes contract simultaneously.

It may be easily shown that the position innervation of the eye muscles develops into motion innervation, when the change of position is continued and, consequently, represents a motion. Fig. 55 gives curves for the reactions of the oblique muscles in the case of a rotation under the same conditions as in Fig. 21. Only the speed of rotation is different in each case. In Fig. 21 the curves are not reciprocal, but in Fig. 55, where the rotation was repeated several times with constant speed, both muscles have written curves of which it may be said that the one is the reflected image of the other.

CHAPTER VIII.

On the Dependence of the Innervation Laws of the Eye Muscles on the Higher Association Nuclei in the Central Nervous System.

As the question of the nervous mechanism of the vestibular eye movements was thoroughly examined in two of my former publications[47, 50] I need only to make a few remarks here.

It has been proved that the labyrinthine stimuli undergo considerable changes in the nervous system before they reach the motor nuclei. The successive modification of the stimuli and their associations with other kinds of innervations take place in *at least* two instances: first, in the nuclei at the floor of the fourth ventricle (so-called vestibular nuclei) and then in the nuclei of the reticular formation in the medulla, pons and midbrain. The nerve cells which play a role in the production of vestibular reflexes are not grouped in separate nuclei for each reflex, as Magnus and his school accepted. The whole body of the substantia reticularis represents an enormous system of association nuclei bound together by short pathways and the destruction of one part of the substantia reticularis changes at once all reflexes. These nuclei may have specialized functions, as future research work perhaps will show, but already it is possible to state with certitude, that the function of each nuclei does not consist in bringing forth a definite reflex pertaining only to this particular nucleus.

The innervation laws of the eye muscles are determined by the physiological activity of the association centers in the substantia reticularis and in the vestibularis nuclei. These laws cannot be something fixed, only dependent on the anatomical connections of the vestibular and eye muscle nuclei. This is easily proved by the fact that lesions in the nerve centers, which condition an abnormal activity of the association nuclei, or lesions in the association nuclei themselves, largely modify the laws, which regulate the activity of the eye muscles. The following two experiments were already published in previous papers[47, 50].

Rabbit of July 2, 1926: Destruction of the vestibular nuclei on both sides from the level of the tub. ac. to the level of the calamus scriptorius (see Fig. 57).

The eyes showed a violent spontaneous nystagmus; the eye movements were conjugated, *i. e.*, they were in each eye in the opposite direction. The plane and direction of the nystagmus was changing continuously, although most frequently the nystagmus was horizontal forwards in the right eye, and diagonal backwards and somewhat downwards in the left eye.

Five hours after the operations the muscles of the left eye were prepared and their activity registered.

All muscles showed nystagmus in the following way:

R. externus and r. internus showed the same nystagmus with *a quick contraction phase; the contractions of both muscles were simultaneous and so were their relaxations.*

R. sup., r. inf., o. sup. and o. inf., however showed nystagmus according to the law of reciprocal innervation of agonists and antagonists; a contraction of the r. sup. and o. sup. took place simultaneously with a relaxation of the r. inf. and o. inf. The spontaneous nystagmus of the r. sup. and o. sup. had a quick contraction phase and that of the r. inf. and o. inf. a quick relaxation phase, and it was smaller in all four muscles than in the horizontal ones.

The nystagmus had no constant amplitude in any of the muscles, there also was no rhythm present, but the corresponding tracings showed that the contractions and relaxations took place at the same time in all muscles.

It was possible to influence the spontaneous nystagmus through rotation innervation of the labyrinth. The curves on Fig. 56 contain the reactions to a rotation to the left with the rabbit in position 4.

It must be said, however, that the influence of the rotation innervation was different every time, because, as mentioned above, the spontaneous phenomena varied continually.

The only effect of the rotation on the horizontal muscles was the increase and decrease of the spontaneous nystagmus. The o. sup. and o. inf. almost did not react to the rotation at all. The r. sup. and r. inf. showed, in addition to small changes in nystagmus, also traces of reflexes due to the centrifugal force.

In order to have a good understanding of the phenomenon, I attached a straw to the right eye and studied at the same time the movements of this eye and the tracings of the muscles of the left eye. The following happened at the beginning of the Curve I of Fig. 56: the nystagmus of the right eye was diagonal back- and downwards; at the end of the rotation between *a* and *b* the nystagmus was directed forwards; from *b* to *c* again back- and downwards.

As the movements of both eyes were conjugated, it is obvious that, at the beginning of the curve, the left eye would have shown a nystagmus directed forwards and, at the end of the rotation, between *a* and *b* a nystagmus directed forwards.

The explanation for the change in direction of the eye nystagmus is seen very clearly in the tracings:—both synergic muscles showed

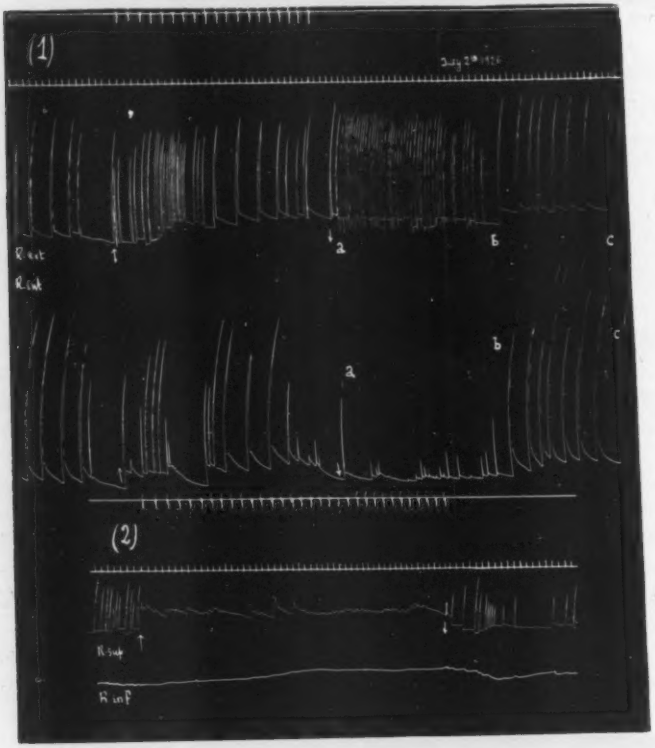

Fig. 56. Spontaneous nystagmus and reactions to rotations on the vertical axis of the horizontal and vertical muscles of the left eye of the rabbit of July 2, 1926. Head in the normal position; rabbit in position 4 of Fig. 26; distance of the head from the axis, 40 c.m.

simultaneous contractions and relaxations, but when the nystagmus was directed forwards, the amplitude of the contraction and, consequently, the force exercised by the r. int. was stronger; and the contractions of the r. ext. were stronger, when the nystagmus was directed backwards and downwards.

MICROSCOPIC ANALYSIS OF THE BRAIN.

The destruction of the vestibular nuclei is very extensive. Caudal to the section represented in Fig. 57, the vestibularis nuclei were totally destroyed. Orally to this section a small part of the Deiters nucleus on the right side was perhaps still functioning and besides the nucleus angularis superior on both sides. On the left side the lesion extends somewhat further orally than on the right side.

In this case the destruction of the vestibularis nuclei conditioned an abnormal activity of the association centers, and as a consequence of this, the laws of innervation of the eye muscles underwent such great changes that the horizontal muscles during nystagmus showed simultaneously strong contractions and relaxations.

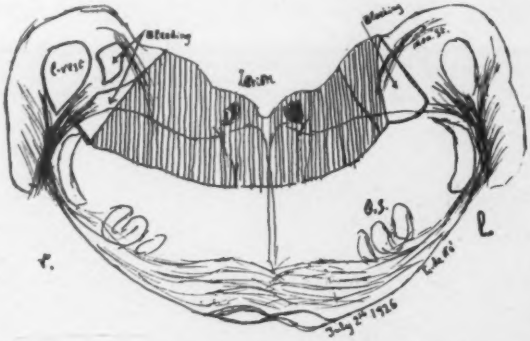

Fig. 57. Cross-section through the medulla of the rabbit of July 2, 1926, showing the oral end of the lesion which destroyed the vestibularis nuclei on both sides. The lesion ends just caudal to the sixth nucleus.

The following experiment is also instructive:

Rabbit of July 15, 1925: As a result of a lesion in pons and midbrain the innervation of the eye muscles changed in the following way: r. int., r. inf. and o. sup. were functionally paralyzed, whereas the r. ext., r. sup. and o. inf. as a reaction to rotations showed strong nystagmus.

Fig. 58 represents tracings of the reactions of the r. ext. and r. sup. The head was not in the normal position in space, but lifted 90° round the bitemporal axis, therefore during the rotation there were present currents only in the vertical semicircular canals.

At the beginning of the rotation, the r. ext. and r. sup. were innervated agonistically. At the end of the rotation the r. sup. showed first a pronounced slow phase (contraction), which was followed

by a quick relaxation; the abnormal state of the nervous centers did obviously not permit the r. ext. to show a nystagmus, at the same time that in the r. sup. a nystagmus with a quick relaxation phase was present, and, therefore, during six seconds the tracings showed in the r. ext. only the slow phase, and it was only later, in the point marked *I*, that this muscle began to show a nystagmus; at the same moment, however, the direction of the nystagmus in the r. sup. reversed and, from there on, this muscle acted as an antagonist to the r. ext. and produced a nystagmus with a quick contraction phase.

We see consequently that, after the rotation, the r. ext. and r. sup. up to the point marked with *I*, acted as synergists and later as antagonists[50].

We have here artificially brought forth, by means of a lesion in the medulla, a phenomenon which may be very often observed in

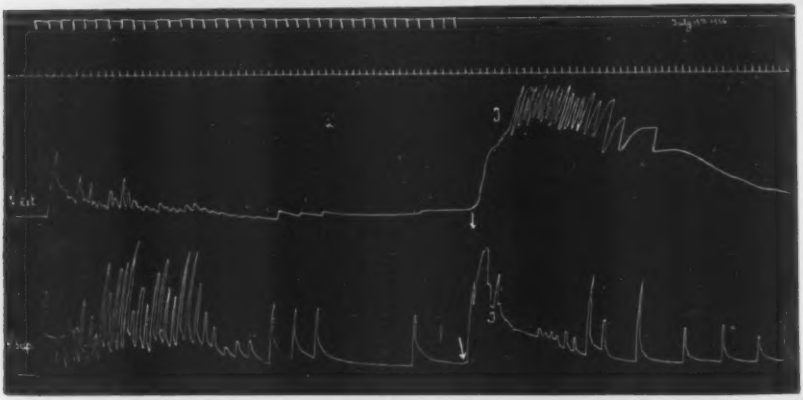

Fig. 58. Rabbit of July 15, 1926. Reactions of the muscles, r. ext. and r. sup., of the left eye to a rotation to the left. Head in position 90° of Fig. 7. Rabbit in position 1 of Fig. 26.

the case of nystagmus as well as in the case of tonic reflexes (see Chapters II and VII). Muscles which, in the case of a certain eye position or eye movement, act as antagonists, are innervated as agonists during another eye position or eye movement. The difference between the normal conditions and the results in this experiment lies in the fact, that here, as a result of the lesions in the medulla and pons, the muscles r. ext., r. sup. and o. inf., were bound together in such a way that a nystagmus of the r. ext. was only possible, when the two other muscles showed nystagmus with a quick con-

traction phase and, consequently, when the r. sup. showed nystagmus with a quick relaxation phase, in the r. ext. only a change of tonus was produced and, thereafter, when the r. ext. started its nystagmus, the nystagmus in the r. sup. changed its direction. Here also the new functional association between both muscles had produced a very considerable modification of the result of the labyrinthine innervation.

We shall deal later again in another paper with the nervous mechanism of the production of the vestibular reflexes, and discuss the theoretical significance of the recorded facts.

SUMMARY.

This paper is a complement to my monograph: "Ausgewaehlte Kapitel der Labyrinthphysiologie," *Ergebnisse der Physiologie*, 32 Bd., 1931, and deals especially with the laws controlling the association of the eye muscles in the case of labyrinth reflexes. Some minor repetitions have been unavoidable in order to make a clear exposition of the facts, but the description of the reflexes and of the mechanism of their production is to be found in the former monograph; in this paper only some complementary facts have been added.

In Chapter I the tonic reflexes on the eye are described.

In Chapter II with the help of different methods the tonic reflexes on the eye muscles are studied, *i. e.*, it is determined which muscles take part in the production of the tonic eye reflexes. Experiments with cutting one or several muscles show that the laws regulating the co-ordination of the muscles must be very complicated, because the muscles may often show strong contractions without the eye being rotated in the direction of their activity. These muscle contractions which really do not bring forth any eye movement must have a twofold purpose, to correct the activity of the motor muscles and to hold the rotation center of the eye fixed in the orbit.

The curves of Figs. 22-24 indicate the state of contraction of each muscle in different head positions in space. These curves show, on one hand, the tonic influence of the labyrinth on the eye muscles and, on the other hand, the state of contraction of the eye muscles when the eye finds itself in one of the positions in the orbit represented in Figs. 7 and 13.

Chapter IV deals with reflexes brought forth by the centrifugal force; a comparison of these reflexes with tonic position reflexes is made.

In Chapter V the rotation reflexes and reflexes produced by excitation of the individual semicircular canals are studied; Figs. 44 and

47 indicate the nystagmus set up in the individual eye muscles by the different kinds of currents in the canals; Figs. 48 and 49 give samples of this nystagmus.

In Chapter VI some problems referent to the combination of motion and position reflexes are outlined.

In Chapters III and VI the laws controlling the co-ordination of the eye muscles during eye positions and eye movements are discussed.

In the case of nystagmus a modified form of the law of reciprocal innervation is valid, but in the cases of the third reaction at the beginning of the rotation and of the postural changes of the muscles during nystagmus the so-called antagonistic muscles often show simultaneous contractions. The same occurs in the case of the corneal reflex, when the six muscles contract simultaneously.

In the case of position reflexes the law of reciprocal innervation as Magnus and de Kleyn have stated it is not valid, and it is doubtful if even the modified form proposed by me for the nystagmus may be applied. In any case it is sure that the co-ordination of the eye muscles is of different nature during nystagmus and during position reflexes.

In Chapter VIII is shown that the innervation laws of the eye muscles change if the activity of the nerve centers undergoes a modification as a consequence of determined lesions. These laws are therefore not dependent on fixed anatomical mechanisms but on the functional activity of the centers because functional activity, for instance inhibition, might produce similar effects as the operative lesion of determined centers or pathways. These experiments bear in themselves an explanation of the fact that the muscles may be co-ordinated in different ways during different kinds of reflexes.

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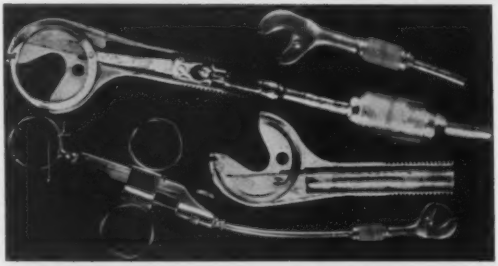
NEW TONSIL SUTURE INSTRUMENT.

Dr. George Ainslie, Portland, Ore.

A suture instrument originally designed to place a suture in the tonsillar fossa, but applicable in any capacity where the instrument could be introduced. It consists of a double casing enclosing a full curved needle sliding in a groove in the casing. The needle at one end has a notch to engage the suture at the distal end of the casing. The other end of the needle (one-half) is divided into two prongs to admit a drawbar which propels the needle forward and backward as desired. This "head" is fastened to the stem by a threaded casing, the drawbar in this casing ending in a ball and fitting in a socket in the connecting rod which slides inside the stem. This ball and socket joint allows turning the head around at any angle desired—



up, down, right or left. The instrument is manipulated by the first two fingers and thumb in rings as in a snare. The suture is placed in a groove at the distal end of the head and held in place by a clip on the handle. On withdrawing the instrument after closing, engaging a suture and pushing needle back in casing, the suture is released from the distal end of the head and is held in the proximal end of the head by the notch. At time of withdrawal, the suture should be released from the clip on the handle.

Only triple (No. 000) catgut (plain) or corresponding sized silk sutures should be used, as too large sutures will naturally cause the needle to jam. Neither should the head be pressed into the tissue too forcibly. If possible, it is best to apply a forceps to the bleeding vessel and suture under or around this point, having a view of what is being done. This instrument manufactured by Pfau's American Instrument Co., whose advertisement appears on page 10.

604 Selling Building.

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